Past and present initiatives on the biological control of *Lantana camara* (Verbenaceae) in South Africa

J-R. Baars & S. Neser

ARC - Plant Protection Research Institute, Private Bag X134, Pretoria, 0001 South Africa

***Lantana camara*, a highly invasive weed in many countries, has been targeted for biological control in South Africa since the early 1960s. An earlier review in 1991 indicated that, despite the establishment of several natural enemy species, the programme has largely been unsuccessful. In this paper we review initiatives undertaken during the 1990s and discuss (i) the status of the natural enemies established on the weed, (ii) factors that have limited the impact of these agents, (iii) the potential of eleven new biocontrol candidates currently under evaluation for release and (iv) the problem of expanded host ranges of imported natural enemies under laboratory conditions. Ultimately, the success of the programme will depend on the establishment of a suite of natural enemies, attacking several parts of the weed, which are able to cope with the extreme variability and wide distribution of *L. camara* in South Africa. Despite the problems associated with the programme, *L. camara* remains a candidate for biological control in South Africa.**

Key words: *Lantana camara*, varieties, biological weed control, natural enemies, host-specificity testing, *Lippia*.

Lantana camara sensu lato (Verbenaceae; Fig. 1), a floriferous, prickly, thicket-forming shrub, which is commonly known as lantana, originates from tropical and subtropical South and Central America (Stirton 1977). As a popular ornamental plant, several varieties (cultivars) of lantana have been widely distributed throughout the tropics, subtropics and warm temperate regions of the world. Following its worldwide introduction, lantana has become naturalized in some 50 countries and is rated as one of the world's worst weeds (Holm *et al.* 1977).

Lantana is an aggressive, vigorously growing weed that tolerates a wide variety of environmental conditions, but thrives better in humid than in dry regions. In South Africa it is presently naturalized in the warm, moist subtropical and temperate regions (Oosthuizen 1964; Stirton 1977) of the Northern Province, Gauteng, Mpumalanga and KwaZulu-Natal, as well as the southern coastal regions of the Eastern and Western Cape Provinces (Fig. 2). Lantana invades river-banks, mountain slopes and valleys, pastures and commercial forests where it forms impenetrable stands that obstruct access and utilization. Through allelopathic suppression of indigenous plant species, lantana invasions also interrupt regeneration processes (Gentle & Duggin 1997a) and reduce the biodiversity of natural ecosystems.

Lantana leaves, stems and fruits contain toxic compounds, notably the pentacyclic triterpenes (Kellerman *et al.* 1996), lantadene A and B (Morton 1994), which if consumed can cause photosensitization, liver and kidney damage, paralysis of the gall bladder, intestinal haemorrhage and death within 1–4 days in cattle, sheep and horses. Livestock previously exposed to lantana are less likely to suffer from the acute symptoms caused by ingestion, while those with no previous exposure are likely to be severely affected. The expected annual impact of cattle mortalities from lantana poisoning in South Africa was estimated to be in excess of R1.7 million (Kellerman *et al.* 1996).

Lantana is an extremely variable entity that presents a complex taxonomic problem (Munir 1996). Its conspicuous variability in general morphology (Howard 1970; Smith & Smith 1982; Cilliers 1987a; Munir 1996), physiology and genetic composition (Spies & Stirton 1982a,b,c; Spies 1984; Spies & Du Plessis 1987), has led to the recognition of hundreds of cultivars or varieties, all of which are classified as *L. camara*. The weed is a polyploid complex, presumably derived from the deliberate hybridization of species in the genus *Lantana* (Stirton 1977) and, subsequent to naturalization in South Africa, hybridization was shown to continue in the field (Spies & Stirton 1982a,b,c). Spies (1984) argued that *L. camara* is in an active phase of evolution, with intermediates in a transitional stage of speciation. Although the species is consid-

Fig. 1
Lantana camara.
(Drawn by R. Weber, National Botanical Institute, Pretoria.)

ered to be unstable, certain varieties dominate in localized areas and remain relatively stable in space and time. Following ecological disturbances, lantana stands may recolonize as a mixture of varieties, but soon revert to the former dominant condition (Spies & Du Plessis 1987).

Chemical and mechanical control of lantana was reviewed by Cilliers & Neser (1991) who concluded that, although very effective, these methods are often labour-intensive and expensive. These control measures usually offer only temporary relief unless continual follow-up treatments are used. Controlled low- to moderate-intensity fires appear to reduce invasions by lantana, and can be an effective, preventative management strategy (Gentle & Duggin 1997b). However, the use of fires is not always a suitable option as infestations are often close to, or in, indigenous forests, grazing lands and plantations. The difficulties and expenses incurred by conventional control measures have fostered the hope that biological control may provide a solution.

The biological control programme, including previously introduced natural enemies on *L. camara* in South Africa, was reviewed by Cilliers & Neser (1991), while other aspects of the weed were reviewed by Swarbrick *et al.* (1995) and Munir (1996). In this paper we mainly review biocontrol initiatives undertaken during the 1990s, notably (i) the status of the natural enemies previously estab-

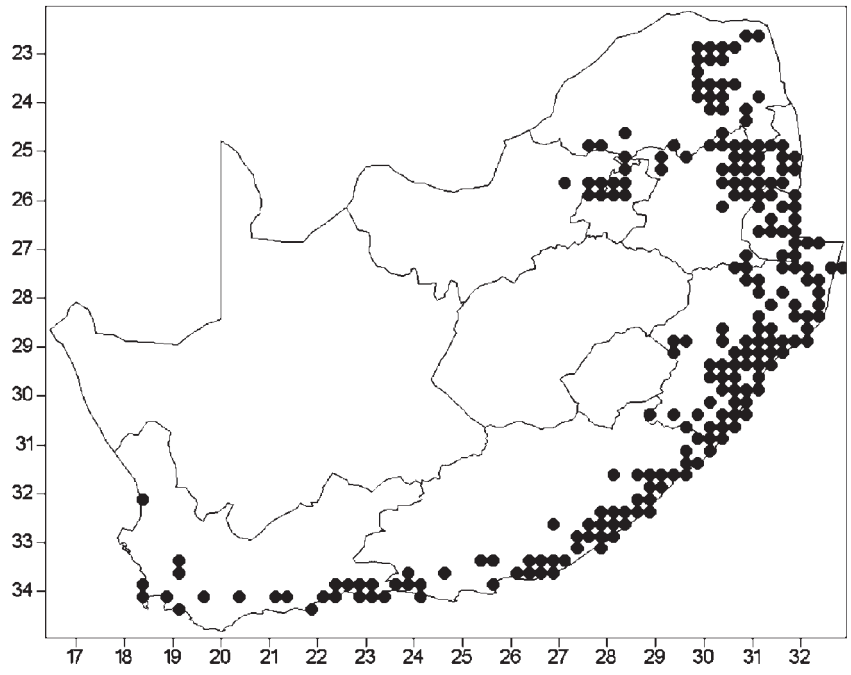

Fig. 2

Distribution of *Lantana camara* in South Africa.

(Drawn by L. Henderson, Plant Protection Research Institute, Pretoria.)

lished on lantana, (ii) the factors that have influenced the efficacy of these natural enemies, (iii) new biocontrol candidates under evaluation for release in South Africa and (iv) the problem of expanded host ranges of natural enemies under laboratory conditions.

STATUS OF NATURAL ENEMIES ESTABLISHED IN SOUTH AFRICA

Biological control of lantana in South Africa was initiated during 1961/62, with the introduction of five natural enemy species (Oosthuizen 1964). However, two of these, *Hypena laceratalis* Walker (= *H. strigata* (F.)) and *Ophiomyia lantanae* (Froggatt), were already established in South Africa (Table 1) and were misidentified during a pre-introductory survey conducted by Oosthuizen (1964). The leaf-feeding moth *Hypena jussalis* Walker was subsequently found to be synonymous with *H. laceratalis,* while specimens of *O. lantanae* were misidentified as *O. rhodesiensis* Spencer, which had been described from Zimbabwe (Cilliers & Neser 1991). *Hypena laceratalis* is widespread and damages seedlings and new growth in summer (Table1). *Ophiomyia lantanae* is widespread and abundant, but has little impact on seed viability (Cilliers & Neser 1991) (Table 1).

The third species, the noctuid moth *Neogalea sunia* (Guenée) (= *N. esula* (Druce), failed to establish despite introductions from Trinidad in 1962 and 1968 and later from Australia in 1983 (Cilliers & Neser 1991). The remaining two species, *Salbia haemorrhoidalis* Guenée and *Teleonemia scrupulosa* Stål became established following the initial releases (Table 2).

Although widely established in South Africa, the flower-feeding pyralid, *S. haemorrhoidalis,* occurs mostly in low numbers and its impact on the weed is unknown. By contrast, the sap-sucking lace bug, *T. scrupulosa,* has become widely established in high numbers throughout the range of *L. camara* in South Africa. It is uncertain whether the later importation and release of additional genetic material from various countries (Table 2) has influenced the efficacy of the tingid in South Africa (Cilliers & Neser 1991). Feeding damage is often extensive, causing periodic defoliation of *L. camara* populations, with damaged plants suffering reductions in seed set (Cilliers 1983, 1987a). Tingid populations and their resultant damage peak in mid-summer but rapidly decline towards winter. *Teleonemia scrupulosa* is considered to be the most effective natural enemy of lantana in South Africa at present.

Two leaf-mining hispine beetles, *Octotoma*

Table 1

Status of natural enemies present on *Lantana camara* in South Africa prior to the initiation of the biological control programme ('generalists' not included).

Order/Family	Natural enemy species	Mode of attack	Status	Limitations
Diptera				
Agromyzidae	*Ophiomyia lantanae* (Froggatt)	Fruit miner	Widely established and abundant	Low impact on seed viability; heavy parasitism
Lepidoptera				
Noctuidae	*Hypena laceratalis*[1] Walker	Leaf chewer	Widely established with considerable damage to seedlings and new growth. Also attacks native *Lippia* and *Priva* species	Larvae are only active during late summer and autumn and are often parasitized
Pterophoridae	*Lantanophaga pusillidactyla*[1] (Walker)	Flower, fruit and seed chewer	Widely established, but present in low numbers. Also attacks native *Lippia* species	Low abundance and possible high levels of parasitism
Tortricidae	*Epinotia lantana*[1] (Busck)	Flower-peduncle and shoot-tip borer	Widely established	Unknown
Gracillariidae	*Cremastobombycia lantanella*[1] Busck	Leaf miner	Widely established, but present in low numbers. Attacks native *Lippia* species	Heavy parasitism

1: scrutiny of identifications, also of specimens from indigenous plants, required.

scabripennis Guérin-Méneville and *Uroplata girardi* Pic, released in the early 1970s (Cilliers & Neser 1991), have become established and coexist in the moist, subtropical areas of the country (Table 2). *Uroplata girardi,* although present in Mpumalanga and the Northern Province, is most successful in the coastal regions of KwaZulu-Natal Province, where it is widely established and reaches high population densities. By contrast, *O. scabripennis* is most abundant at inland sites, where populations peak infrequently in localized areas. Populations of both species reach damaging levels during mid-summer and often cause the defoliation of lantana stands (Cilliers 1987b), but the plants may recover rapidly. Although a third leaf-mining beetle, *Octotoma championi* Baly, failed to establish after releases in 1978 (Cilliers & Neser 1991), further releases were made at an inland, low altitude site near Nelspruit (Mpumalanga Province) in 1995. The population persisted in low numbers for the following two seasons, but its present status is unknown (Table 2).

The leaf-mining fly, *Calycomyza lantanae* (Frick), released in 1982 (Cilliers & Neser 1991) has also become widespread (Table 2). Populations initially established in the warm, subtropical regions and subsequently became widely established in the temperate regions. The blotch mines initiated by the flies appear more abundant in the subtropical regions, with most of the damage visible on actively-growing plants, seedlings and coppice growth. Additional material was released in 1989 (Table 2) but its effect on the established populations is unknown. The impact of *C. lantanae* populations on lantana infestations is unknown, but is reduced by the extensive larval parasitism observed throughout the fly's range.

Besides the three species already mentioned, a further two moths were released in South Africa but were later found to have already been established (Table 1). Both were introduced via Hawaii in 1984 (Cilliers & Neser 1991; Julien & Griffiths 1998) and neither has inflicted appreciable damage on the weed. Larvae of the plume moth *Lantanophaga pusillidactyla* (Walker) feed on the bases of the flowers, binding them together. Feeding damage causes a typical streak of aborted flowers among the cluster, leaving the other flowers to develop normally (Perkins & Swezey 1924). Larvae of the tortricid moth *Epinotia lantana* (Busck) attack the flowers, hollowing out the receptacle, and also burrow into the young shoot tips (Perkins & Swezey 1924).

Although never deliberately introduced, the tineid moth *Cremastobombycia lantanella* Busck is widely established in South Africa (Table 1). The larvae initiate serpentine leaf mines, which later develop into 'blister'mines, and later pupate in spindle-shaped, ribbed cocoons, which are suspended within the 'blisters'. Populations are usually low, suffer heavy parasitism, and also cause negligible damage to lantana. Moths believed to be *C. lantanella* and *L. pusillidactyla* have been reared from different indigenous *Lippia*

Table 2

Status of natural enemies released and established on *Lantana camara* in South Africa.

Order/ Family	Natural enemy species	Origin	Main releases	Mode of attack	Status	Damage inflicted
Coleoptera						
Chrysomelidae	*Octotoma scabripennis* Guérin-Méneville	Mexico via Hawaii via Australia	1971	Leaf miner	Established in the warm, moist eastern range of lantana. Abundant in localized inland areas	Extensive defoliation, but localized
	Octotoma championi Baly	Costa Rica via Australia	1978 1995	Leaf miner	Persisted in low numbers for two seasons after the last release. Establishment unconfirmed	Unknown
	Uroplata girardi Pic	Paraguay via Hawaii via Australia	1974 1983	Leaf miner	Abundant in KwaZulu-Natal coastal regions. Present in low numbers in the warm, moist inland range of lantana	Extensive defoliation in coastal regions
Diptera						
Agromyzidae	*Calycomyza lantanae* (Frick)	Trinidad via Australia Florida, USA	1982 1989	Leaf miner	Widely established in low numbers. Heavily parasitized	Unknown
Hemiptera						
Tingidae	*Teleonemia scrupulosa* Stål	Mexico via Hawaii via Australia via Mauritius Florida, USA	1961 1971 1984 1989	Flower and leaf sucker	Widely established in large numbers across the entire range of lantana; severe damage sporadic	Complete defoliation and abortion of flowers in subtropical regions
Lepidoptera						
Pyralidae	*Salbia haemorrhoidalis* Guenée	Cuba via Hawaii	1962	Flower and fruit feeder	Widely established in low numbers. Reared from native *Lippia*species	Unknown

species. It is possible that these two species and perhaps even *H. laceratalis* and *E. lantana* were inadvertently introduced into South Africa together with lantana plants, although they may be indigenous. The geographic range, correct identities and status of the different lepidopterans associated with lantana in South Africa are in need of revision.

FACTORS AFFECTING THE IMPACT OF ESTABLISHED AGENTS

Despite the establishment of several natural enemies on *L. camara* in South Africa (Oosthuizen 1964; Cilliers & Neser 1991), the biological control programme in South Africa has had limited success. This has largely been attributed to the genetic diversity of lantana, which has made it an extremely variable target weed. The diversity of varieties presents the natural enemies with several morphological and physiological barriers to utilization (Cilliers 1983; Neser & Cilliers 1990; Cilliers & Neser 1991). Indeed, the introduced complex of *L. camara* is a man-made polyploid entity (Stirton 1977), which is far removed from the parent species occurring in its native range. Introduced natural enemies are therefore poorly adapted to cope with the diversity of 'new' entities naturalized in the countries of introduction.

Several natural enemies (*e.g. T. scrupulosa* and *C. lantanae*) were reported to display preferences for certain varieties of lantana (Radunz 1971; Harley & Kassulke 1974; Harley *et al.* 1979; Cilliers 1987b; Cilliers & Neser 1991). In some cases (*e.g. E. xanthochaeta*), agents have reportedly failed to establish because of the phenomenon of varietal resistance or reduced compatibility (Cilliers & Neser 1991). Agents from different isolated varieties of *L. camara,* or from other species such as *L. tiliaefolia* (Winder & Harley 1983), may thus all be considered as 'new' associations when deployed against the plants in South Africa. Consequently, the interactions between the various natural enemies and the different lantana varieties are complex and difficult to predict.

Harley & Kassulke (1974) and Cilliers & Neser (1991), amongst others, have thus emphasized the need to import different 'strains' of the natural enemies already released, so as to increase the number of lantana varieties attacked. However, the distinction must be made between agents previously established and those that failed to establish. Since little is known about the extent to which established agents have realized their

potential, importations of new genetic material (*e.g. T. scrupulosa*) may not necessarily alter an agent's status in South Africa. Unless the impacts of established natural enemies are well quantified, it seems inappropriate to introduce new material. Neser & Cilliers (1990) highlighted the difficulties of monitoring new genetic material in large, well-established populations, which may result in inconclusive evidence unless suitable techniques are used. By contrast, the re-importation of new 'strains' of species that failed to establish, collected from different species in the lantana complex and from climates that match target release sites, is expected to improve the chances of establishment (Neser & Cilliers 1990; Cilliers & Neser 1991).

To increase the number of lantana varieties attacked in South Africa, Neser & Cilliers (1990) suggested that local varieties should be exposed to the natural enemies within the native range of *L. camara*. This would afford several advantages but would depend on detailed comparative performance studies on the South African varieties. These would indicate the natural enemies that can cope with the different varieties as well as the degree of suitability of their 'new' hosts.

High rates of parasitism in the field have been observed for *C. lantanae, C. lantanella, O. lantanae* and *H. laceratalis* and appear to significantly reduce the efficacy of these natural enemies in South Africa. *Eutreta xanthochaeta* is also known to be heavily parasitized in other countries where it has established (Daun & Messing 1996), suggesting that the recruitment of native generalist parasitoids may have contributed to its failure to establish in South Africa. However, the possibility of heavy parasitism by native parasitoids should not deter releases of new species or 'strains' of natural enemies. Parasitized populations could still inflict significant damage, provided that the populations are able to proliferate and survive seasonal and other adversities.

NEW BIOCONTROL CANDIDATES UNDER EVALUATION

The biology, host specificity and potential of several species that are being evaluated for release in South Africa (Table 3) are summarized below.

Aceria lantanae (Acari: Eriophyidae)

The eriophyid mite, *Aceria lantanae* (Cook), is known to cause two characteristic kinds of damage to *Lantana* species in South and Central America (Flechtmann & Harley 1974). In South American countries it causes 'crinkle' galls on the leaf surface (Flechtmann 1973). In Central America it distorts flower buds into inflorescence galls comprising a mass of tiny green leaves (Keifer & Denmark 1976). These two symptoms are geographically distinct and seldom coexist, with reported incidences of both kinds of symptoms from Florida (Cromroy 1983), Mexico (Palmer & Pullen 1995) and Venezuela. Although regarded as morphologically identical, mites inducing the two symptoms appear to be distinct and may constitute separate biotypes or species.

The lantana inflorescence mite was first imported from Florida, USA (Craemer 1989). Although attempts to rear the mite on local lantana varieties in quarantine were largely unsuccessful, developing colonies induced limited symptoms. In 1996, a colony was initiated from rooted material imported from Florida, but later died out as successive daughter plants were severely damaged by excessive gall formation. Mite-induced galls appear to act as metabolic sinks, but also form in place of flowers and thereby primarily reduce seed set. Heavy infestations of the inflorescence mite observed in Florida, USA, after an exceptionally wet season in 1998, resulted in large stands of lantana being devoid of mature flowers. Following introductions from several countries (Table 3) in 1997, a mixture of flower gall mite colonies developed characteristic symptoms on several South African and Australian lantana varieties in quarantine (Urban, unpubl.). Successful gall induction appears to require a combination of suitable physiological (differentiating flower buds on an actively-growing plant) and environmental conditions (high humidity) during infestation. Host-specificity screening is underway. Additional material was imported from Mexico and Venezuela in 1998 (Table 3), in an attempt to boost the genetic base of the laboratory culture.

Falconia intermedia (Hemiptera: Miridae)

Two separate laboratory cultures of *Falconia intermedia* (Distant) were collected in Jamaica in 1994 and in Guatemala in 1997 (Neser, unpubl.). This species is endemic to Central America where it is associated with several species in the *L. camara* complex (Palmer & Pullen 1995, 1998).

Adults and nymphs are highly active and mobile, and feed on the undersides of leaves. Feeding damage causes chlorosis, characterized by the stippling of the upper leaf surfaces, and can cause them to desiccate and abscise. Eggs are deposited singly or in small groups, on the

Table 3

Status of biocontrol candidates recently evaluated for release on *Lantana camara* in South Africa.

Order/ Family	Natural enemy species	Date imported	Origin	Status
Acari				
Eriophyidae	*Aceria lantanae* (Cook)	1989	Florida, USA.	Imported for culturing on local lantana varieties and undergoing biological studies
		1996	Florida, USA;	
		1997[1]	Florida, USA. Jamaica; Mexico	New material imported as separate 'strains' to determine compatibility with local lantana varieties. Undergoing host-specificity tests
		1998[1]	Mexico; Venezuela	
Hemiptera				
Miridae	*Falconia intermedia* (Distant)	1995[1]	Jamaica	Released in April 1999
		1997[1,2]	Guatemala.	Imported to provide new genetic material for laboratory culture
Tingidae	*Teleonemia vulgata* Drake & Hambleton	1996[1]	Brazil	Undergoing host-specificity tests
Membracidae	*Aconophora compressa* Walker	1995[1]	Mexico via Australia	Undergoing host-specificity tests
		1997	Guatemala	Guatemalan culture (only) terminated
Coleoptera				
Apionidae	*Coelocephalapion* sp.	1997[1]	Mexico, Cárdenas	Undergoing biological studies and host-specificity screening Appears acceptable for release in South Africa
		1998[1,2]	Mexico, Veracruz	Imported to provide new genetic material for laboratory culture
Chrysomelidae	*Omophoita albicollis* Fabricius	1993	Jamaica	Rejected because of wide host range under laboratory conditions Culture terminated
	Charidotis pygmaea Buzzi	1994[1]	Colombia via Australia	Undergoing performance trials on local lantana varieties for comparison with performance on *Lantana montevidensis*
		1998[1]	Colombia via Australia	
	Alagoasa prob. *quadrilineata* (Harold)	1997[1]	Mexico	Undergoing biological studies and host-specificity screening
	?Longitarsus sp.	1996	Trinidad; Florida	Culture died in quarantine
		1997	Mexico	Culture died in quarantine
		1998[1]	Mexico, Veracruz	Undergoing biological studies and developing culturing techniques
	?L. columbicus Harold	1998[1,2]	Venezuela	Undergoing biological studies and developing culturing techniques
Diptera				
Agromyzidae	*Ophiomyia camarae* Spencer	1995	Florida, USA	Culture died in quarantine
		1996	Trinidad	Culture died in quarantine
		1997[1]	Florida, USA; Mexico	Undergoing host-specificity tests. Appears acceptable for release in South Africa
		1998[1,2]	Florida, USA	New material imported to boost the quarantine culture
Tephritidae	*Eutreta xanthochaeta* Aldrich	1998[1]	Hawaii	Undergoing biological studies and host-specificity tests

1: importations from which the current laboratory cultures originate.
2: separate laboratory culture maintained.

undersides of the leaves. Under laboratory conditions the eggs hatched after about 13 days and the nymphs (there are five instars) completed their development in about 14 days; adults lived for up to two months and laid about four eggs per day.

Nymphs of *F. intermedia* completed their development on *L. camara* and some native species of *Lippia* (Verbenaceae). No survival and development occurred on the native *Lantana rugosa* Thunb. or the introduced ornamental *Lantana montevidensis* (Sprengler) Briquet, and performance was poor on the introduced *Lantana trifolia* L. In adult starvation trials *F. intermedia* had significantly higher rates of survival and egg production on *L. camara* than on the various *Lippia* species. During multi-choice trials, *L. camara* was consistently selected as the preferred host plant for feeding and oviposition. Based on these results, *F. intermedia* was cleared for release, and released, in South Africa in April 1999.

Teleonemia vulgata (Hemiptera: Tingidae)

A culture of the sap-sucking lace-bug, *Teleonemia vulgata* Drake & Hambleton, was collected in 1996 in Rio de Janeiro, Brazil, near the only locality from which this species was previously recorded

(Drake & Ruhoff 1965). Damage in the field appears similar to that caused by *T. scrupulosa.* Several species of *Teleonemia* are associated with the *Lantana* species complex in South and Central America, and some have been released as biocontrol agents in various countries (Julien & Griffiths 1998). With the exception of *T. validicornis* Stål (Harley & Kassulke 1971), all six *Teleonemia* species that were studied proved suitable for release. *Teleonemia vulgata* has not been previously evaluated as a biocontrol agent against *L. camara.*

Adults and nymphs prefer to feed on flowers, but readily feed on leaves and vegetative buds. Eggs are inserted singly or in small clusters into the ventral veins and periphery of leaves, and into the flower peduncle. Eggs take about 14 days to hatch and the nymphs pass through five instars, taking about 15 days to complete their development. Feeding damage results in the abortion of florets and the desiccation and abscission of leaves.

During no-choice tests, nymphs completed normal development on *L. camara, L. rugosa, L. trifolia, L. montevidensis,* and different indigenous *Lippia* species. Survival and development on the native *Priva cordifolia* Druce (Verbenaceae) was low, indicating its unsuitability as a host. Preliminary adult starvation trials on these plant species indicated that ovariole development was better on *L. camara,* resulting in a higher deposition of fat reserves, well-developed ovaries and eggs. During choice tests, gravid females preferred to feed and oviposit on *L. camara,* with comparatively fewer eggs deposited on the other plant species. Additional multi-choice trials are to be completed before *T. vulgata* may be considered for release.

Aconophora compressa (Hemiptera: Membracidae)

A culture of the stem-sucking membracid, *Aconophora compressa* Walker, from Cuernavaca, Mexico, was obtained from the Queensland Department of Natural Resources, Australia, in 1995 (Table 3). This species is endemic to the Neotropics (Palmer *et al.* 1996). Specimens collected in 1997 (Neser, unpubl.) in Guatemala appeared somewhat different from the Mexican material and a separate quarantine culture was maintained, but later destroyed when it was confirmed to be the same species.

Adults feed on the stems of lantana and remain gregarious during the pre-oviposition period. Females then disperse to insert the eggs into actively-growing stems, forming egg cases of about 70 eggs that are covered by a protective froth. The females tend the egg cases and emerging nymphs, until these complete their development (Palmer *et al.* 1996). Nymphs undergo five instars and display a variable rate of development, ranging from 28–108 days in the greenhouse. Feeding damage causes flowers to abort and shoot tips to wilt and die back, often causing long sections of thick stems to die.

Host-specificity tests indicated that among the different species of *Lantana, A. compressa* was specific to *L. camara,* confirming the results of Palmer *et al.* (1996) in Mexico and Australia. Starvation tests showed that feeding on a number of indigenous *Lippia* species allowed ovariole development, oviposition and high rates of nymphal emergence, similar to that on *L. camara.* However, preliminary multi-choice trials with inexperienced adults revealed preferences for *L. camara.* Species of *Lippia* may thus be able to serve as marginal hosts under field conditions and further performance and choice trials will be conducted before *A. compressa* is considered for release in South Africa.

Coelocephalapion sp. (Coleoptera: Apionidae)

The petiole-boring apionid, an undescribed species of *Coelocephalapion* (Kissinger, pers. comm.), was first collected in Cardenas, Tabasco Province, Mexico, during a survey in 1997, and subsequently at a number of sites in Veracruz, Mexico, in 1998.

Adults feed on the leaves of lantana, and eggs are inserted into the leaf petiole and flower peduncle. Larvae burrow for a short distance into the plant tissue and induce a small gall. The later instars remain relatively sedentary and feed on callus tissue within the gall. Larvae pass through four instars and pupate inside the gall, and adults emerge from a small exit hole chewed in the gall. The life cycle from egg to adult is approximately 30–35 days in the laboratory and the adults live for 4–5 months. Galls induced on the leaf petiole disrupt the supply of liquids and may cause small leaves to desiccate and abscise. Flower galls appear to prevent the development of seeds in the laboratory.

Preliminary tests suggested that the weevils are host specific and perform best on *L. camara.* During starvation trials, adults fed and oviposited on the two introduced species, *L. montevidensis* and *L. trifolia,* and on five indigenous species, namely *Lantana rugosa, Lippia javanica* Spreng., *Lippia rehmannii* Pearson, *Lippia wilmsii* Pearson and *Lippia scaberrima* Sond. Although a number of

eggs were deposited on these plants during these trials, far fewer larvae completed their development on them than on *L. camara.* During multi-choice tests, adults consistently preferred to feed and oviposit on lantana. The specific oviposition behaviour of the apionid is thought to limit the number of suitable hosts. The results so far indicate that the apionid may be acceptable for release in South Africa.

Charidotis pygmaea (Coleoptera: Chrysomelidae)

The leaf-feeding tortoise beetle, *Charidotis pygmaea* Buzzi, was imported into South Africa from Brazil, via Australia, in 1994 (Table 3). Adults and larvae feed on the leaves, causing characteristic longitudinal feeding scars on the upper leaf surfaces. Eggs are deposited singly on leaves, semi-embedded into the lower epidermis and covered by a hardened froth excretion. Protective froth extends from the posterior end of the egg and forms a raised covering over the egg, most likely functioning as protection against parasitoids. The larvae undergo five instars, lasting about 38 days to pupation, which occurs on the leaf surface.

Although originally collected on *Lantana tiliaefolia* (Swarbrick *et al.* 1995), one of the closely related species in the *L. camara* complex and very similar to the weedy forms, *C. pygmaea* was thought to be potentially specific to *L. camara.* However, adults performed better on the introduced *L. montevidensis* (creeping lantana) than on various *L. camara* varieties. Survival and development also occurred on the indigenous *L. rugosa* and various *Lippia* species, but performance was poor relative to that on *L. montevidensis* and *L. camara* (Sparks, unpubl.). Various sterile forms of *L. montevidensis,* and hybrids, have been introduced into South Africa via the ornamental trade and are popular garden plants. The fertile form in Australia is regarded as invasive (Munir 1996) and was also targeted for biological control with the release of *C. pygmaea* (Julien & Griffiths 1998). Since *C. pygmaea* appears to be better suited to *L. montevidensis* than to local South African lantana varieties, it seems unlikely that it will be further considered for release in South Africa.

Omophoita albicollis (Coleoptera: Chrysomelidae)

A culture of the leaf-feeding flea beetle, *Omophoita albicollis* Fabricius, was collected in Jamaica in 1993. Adults feed voraciously on flowers and leaves and deposit eggs under leaf litter on the soil surface. Larvae emerge from the leaf litter and feed on recently abscised leaves, or on leaves on branches near the ground. Larvae pass through three instars, taking 21–25 days to complete their development, and then burrow into the soil to pupate within a hardened chamber. In the laboratory adults emerge from the soil after about 10 days (Sparks, unpubl.).

During starvation trials, larvae survived and developed on several species of Verbenaceae, including *L. trifolia,* several indigenous *Lippia* species and *Phyla nodiflora* Greene. Larvae also developed on several indigenous and economically important species in the Lamiaceae. During multi-choice trials, adults fed on several species of Verbenaceae and Lamiaceae and caused damage similar to that on *L. camara.* The unacceptably wide host range of *O. albicollis* resulted in its rejection as a biocontrol candidate for release in South Africa (Sparks, unpubl.) and the laboratory culture was terminated.

Alagoasa prob. *quadrilineata* (Coleoptera: Chrysomelidae)

A supply of the leaf-feeding flea beetle, *Alagoasa* prob. *quadrilineata* (Harold), was collected in Catemaco, Mexico in 1997 (Neser, unpubl.). During a survey in Mexico in 1998 (Baars & Sparks unpubl.), similar adults were collected on members of the *L. camara* complex in the Yucatán, Campeche, Tabasco and Veracruz provinces.

Adults and larvae feed on the leaves, and larvae pupate in the soil. The adults have three distinct colour and pattern forms (uniform, blotched and striped). Preliminary host-specificity tests indicated that survival and development occurred on closely related plants within the Verbenaceae (Sparks, unpubl.). *Alagoasa* prob. *quadrilineata* is at an early stage of evaluation and further studies on its biology and host-specificity will be conducted before it is considered for release in South Africa.

?Longitarsus sp. (Coleoptera: Chrysomelidae)

Adults of the flea beetles believed to belong to the genus *Longitarsus* were collected from Trinidad and Florida in 1996 (Table 3); they failed to establish in the laboratory. A further culture of a *?Longitarsus* sp., collected in Mexico in 1997 persisted for several generations in the laboratory but the adults did not reappear after the first winter. Another culture was collected from Veracruz in Mexico in 1998 and still persists in the laboratory. A culture of a flea beetle, provisionally identified as

Longitarsus columbicus columbicus Harold, was collected in Maracay, Venezuela in 1998. This species was previously recorded on *Lantana* spp. in Venezuela (Savini 1997). The identity and possible conspecificity of the specimens collected in the various countries they were not determined and were maintained as separate cultures.

Adults of *?Longitarsus columbicus columbicus* feed on the leaves of lantana, and deposit their eggs in the leaf litter. Emerging larvae burrow into the soil and feed externally on secondary rootlets. Larvae pupate in hardened cases near the soil surface. The immature stages require about 2 months for development in the laboratory, and the adults lived in excess of 2 months. Reliable culture techniques are being developed before host-specificity tests can be conducted.

Ophiomyia camarae (Diptera: Agromyzidae)

The herringbone leaf miner, *Ophiomyia camarae* Spencer, originates from South and Central America. Adult flies are small and very active, usually inserting a single egg into the epidermal tissue on the abaxial aspect of leaves. The emerging larva burrows into the mesophyll tissue, typically towards the midrib of the leaf. The larva then burrows laterally, in a characteristic 'herring-bone' pattern, into the leaf lamina, and also into the petiole. The late instar larva usually burrows towards the tip of the leaf, or elsewhere near the edge of the leaf, where pupation occurs. Leaves damaged by the larvae may abscise prematurely, and larval development is completed in abscised leaves. High populations were recorded in Florida, USA (Stegmaier 1966), and were similarly observed there during 1987 and 1998.

Characteristic leaf mines have been recorded on *L. tiliaefolia* in Brazil (Winder & Harley 1983), on *L. camara* in Mexico (Palmer & Pullen 1995), Trinidad and Florida (Stegmaier 1966), on *L. trifolia* in Venezuela and on unidentified *Lantana* species in Jamaica, Guatemala and Brazil. Although the identities of the flies were not all confirmed, it appears that *O. camarae* is associated with various species of the genus *Lantana* and is able to utilize them as hosts across its native geographical range. Preliminary host-specificity trials confirmed this association and the fly has performed well on several local lantana varieties. Although oviposition and larval development occurred on some indigenous *Lippia* species, performance was far better on *L. camara* (Simelane, unpubl.) and the fly will be considered for release.

Eutreta xanthochaeta (Diptera: Tephritidae)

The stem-galling tephritid, *Eutreta xanthochaeta* Aldrich, was one of the first natural enemies released against *L. camara* in Hawaii in 1902 (Perkins & Swezey 1924). The fly was first imported into South Africa in 1983 (Cilliers & Neser 1991) (Table 3) and was considered to be safe for release. It was reared in quarantine for one generation and released in very low numbers at one site near Hartbeespoort (North-West Province). Although galls were initially recovered, the fly failed to establish, probably because too few were released, and on lantana varieties with which they may also have been incompatible (Cilliers & Neser 1991). A new culture was imported from Hawaii in 1998 and although previously released, is undergoing biology studies and host-range tests in quarantine. These tests will incorporate indigenous plant species that were not tested previously, because of the observed tendency of other natural enemies of lantana to have expanded host ranges, and in the light of present environmental legislation pertaining to biocontrol agents in South Africa.

Adult females insert eggs into actively-growing shoot tips. Larvae burrow into the stem, causing the shoot to swell and form an elongated or round gall of up to 15 mm in diameter. Rapid growth of the apical stem above the gall is initially stunted, but growth may resume after the flies emerge if the shoot tip has not died (Perkins & Swezey 1924). Larvae feed on the proliferated gall tissue, taking up to 45 days to complete development in the greenhouse. Pupation occurs within the gall, and adults emerge through an epidermal window prepared by the larva.

Preliminary quarantine tests indicate that *E. xanthochaeta* oviposits on several lantana varieties, all of which appear suitable for larval development. Oviposition and development also occurs on indigenous *Lippia* species (Klein, unpubl.) and performance and choice trials will be conducted before further releases in South Africa are considered.

EXPANDED LABORATORY HOST RANGES OF NATURAL ENEMIES

Recent host-specificity tests have indicated that most of the natural enemies currently under evaluation accepted related native plant species to varying degrees under laboratory conditions. Ironically, natural enemies selected for the biocontrol of lantana are required to cope with the

variability of the weed, but are also required to not accept closely related species. Two species in the genus *Lantana* and four in the genus *Lippia* considered native to South Africa (Arnold & De Wet 1993), are generally accepted as hosts by the recently imported natural enemies of lantana under laboratory conditions. Some insect species (*e.g. A. compressa* and *C. pygmaea*), which were acceptable for release in Australia (Julien & Griffiths 1998), may accept and marginally affect these non-target indigenous species in South Africa.

To reconcile physiological and true host ranges, laboratory and field studies were conducted on species that have been established in South Africa for decades. The tingid, *T. scrupulosa,* displayed non-host specific behaviour in the laboratory, feeding and developing on a wide range of species within the Verbenaceae. However, preliminary studies provided no evidence of an extended host range in the field where *T. scrupulosa* was observed to display only limited feeding on some native *Lippia* species. These studies provided further evidence of the conservative nature of laboratory tests and suggest that extended laboratory host ranges are often, as in many biocontrol programmes worldwide, not realized under field conditions.

Although some of the natural enemy species presently under evaluation (*e.g. Coelocephalapion* sp.) do not accept certain closely related native species, most others appear to perform well on several closely related species. *Aconophora compressa* (Palmer *et al.* 1996) and *T. scrupulosa* (Harley & Kassulke 1971) have been recorded on *Lippia* species in their native range, but detailed performance studies on other promising species (*e.g. F. intermedia*) in the laboratory have indicated that although various *Lippia* species are acceptable, performance was poor relative to that on *L. camara.* One solution to determining the acceptability of expanded laboratory host ranges would be to accept possible limited feeding on such non-target species in the field, as an ecologically justifiable 'trade-off' against the benefits of releasing agents that have the potential to suppress such an environmentally damaging target weed. Alternatively, the number of new natural enemies that will ultimately be considered acceptable for release in South Africa will be limited, with obvious constraints on the biocontrol programme.

CONCLUSIONS

The success of the biocontrol programme against lantana will depend on a suite of natural enemies that can cope with the extreme variability and wide distribution of the weed in South Africa, without compromising native Verbenaceae. It is apparent that the insect agents currently established on lantana in South Africa do not exert sufficient control and that additional natural enemies are required. In this respect, Cilliers & Neser (1991) suggested a possible shift in the selection of new natural enemies, in which stem borers, root feeders and flower feeders should take precedence over leaf feeders.

Natural enemies established in South Africa, notably *T. scrupulosa, O. scabripennis* and *U. girardi,* periodically defoliate lantana stands (Cilliers 1987b), but fail to sustain these levels of damage to the photosynthetic niche, and thus the resource production by the plant. This niche is therefore in need of additional herbivore pressure and new leaf feeders should also be considered. However, several niches are not affected by natural enemy attack and the suite of candidate biocontrol agents should comprise species that attack as many parts of the plant as possible. In pursuit of this objective, natural enemies under consideration include feeders on leaves, stems, petioles and shoots, flowerbuds and roots. The abundance of potential agents suggests that, despite the problems associated with the programme, *L. camara* remains a candidate for biological control in South Africa.

ACKNOWLEDGEMENTS

We thank A.J. Urban, H. Klein, H.E. Sparks, F. Heystek and D.O. Simelane of the Plant Protection Research Institute for technical and research assistance and for the use of unpublished data. We are also grateful to M.P. Hill, T. Olckers and A.J. Urban (all of PPRI) for comments on the manuscript. We are grateful to various organizations for providing financial support for the research programme against lantana, including the National Department of Agriculture, Department of Water Affairs and Forestry, H.L. Hall & Sons, Hans Merensky Foundation and the Agricultural Research Council of South Africa.

REFERENCES

ARNOLD, T.H. & DE WET, B.C. 1993. Plants of southern Africa: names and distribution. *Memoirs of the Botanical Survey of South Africa* **62**: 596–637.

CILLIERS, C.J. 1983. The weed, *Lantana camara* L., and the insect natural enemies imported for its biological control into South Africa. *Journal of the Entomological Society of Southern Africa* **46**: 131–138.

CILLIERS, C.J. 1987a. Notes on the biology of the established insect natural enemies of *Lantana camara* L. (Verbenaceae) and their seasonal history in South

Africa. *Journal of the Entomological Society of Southern Africa* **50**: 1–13.
CILLIERS, C.J. 1987b. The evaluation of three insect natural enemies for the biological control of the weed *Lantana camara* L. *Journal of the Entomological Society of Southern Africa* **50**: 15–34.
CILLIERS, C.J. & NESER, S. 1991. Biological control of *Lantana camara* (Verbenaceae) in South Africa. *Agriculture, Ecosystems and Environment* **37**: 57–75.
CRAEMER, C. 1989. Eriophyidae (Acari) as potential control agents of South African weeds, with descriptions of a new species of *Tegonotus* Nalepa and of *Paraphytoptus* Nalepa. M.Sc. thesis, Rand Afrikaans University, Johannesburg.
CROMROY, H.L. 1983. Potential use of mites in biological control of terrestrial and aquatic weeds. In: Hoy, M.A., Cunningham, G.L. & Knutson, L. (Eds) *Biological Control of Pests by Mites.* 61–66. University of California, Berkeley.
DAUN, J.J. & MESSING, R.H. 1996. Response of two opiine fruit fly parasitoids (Hymenoptera: Braconidae) to the lantana gall fly (Diptera: Tephritidae). *Biological Control* **25**: 1428–1437.
DRAKE, C.J. & RUHOFF, F.A. 1965. Lacebugs of the world: a catalog (Hemiptera: Tingidae). *Bulletin of the United States National Museum* **243**: 1–634.
FLECHTMANN, C.H.W. 1973. On an eriophyid mite (Acari) from lantana from Brazil. *Anais da Sociedade Entomológica do Brasil* **2**: 109–110.
FLECHTMANN, C.H.W. & HARLEY, K.L.S. 1974. Preliminary report on mites (Acari) associated with *Lantana camara* L. in the Neotropical region. *Anais de Sociedade Entomológica do Brasil* **3**: 69–71.
GENTLE, C.B. & DUGGIN, J.A. 1997a. Allelopathy as a competitive strategy in persistent thickets of *Lantana camara* L. in three Australian forest communities. *Plant Ecology* **132**: 85–95.
GENTLE, C.B. & DUGGIN, J.A. 1997b. *Lantana camara* L. invasions in dry rainforest-open ecotones: the role of disturbances associated with fire and cattle grazing. *Australian Journal of Ecology* **22**: 298–306.
HARLEY, K.L.S. & KASSULKE, R.C. 1971. Tingidae for biological control of *Lantana camara* [Verbenaceae]. *Entomophaga* **16**: 389–410.
HARLEY, K.L.S. & KASSULKE, R.C. 1974. The suitability of *Phytobia lantanae* Frick for biological control of *Lantana camara* in Australia. *Journal of the Australian Entomological Society* **13**: 229–233.
HARLEY, K.L.S., KERR, J.D. & KASSULKE, R.C. 1979. Effects in S.E. Queensland during 1967–72 of insects introduced to control *Lantana camara. Entomophaga* **24**: 65–72.
HOLM, L.G., PLUCKNETT, D.L., PANCHO, J.V. & HERBERGER, J.P. 1977. *The World's Worst Weeds.* The University Press of Hawaii, Honolulu.
HOWARD, R.A. 1970. *Lantana camara* – a prize and a peril. *American Horticultural Society* Winter: 31–36.
JULIEN, M.H. & GRIFFITHS, M.W. 1998. *Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds.* 4th Edition. CABI Publishing, UK.
KEIFER, H.H. & DENMARK, H.A. 1976. *Eriophyes lantanae* Cook (Acarina: Eriophyidae) in Florida. Florida Department of Agricultural Services, Division of Plant Industry, Entomology Circular No. 166, 2 pp.
KELLERMAN, T.S., NAUDE, T.W. & FOURIE, N. 1996. The distribution, diagnoses and estimated economic impact of plant poisonings and mycotoxicoses in South Africa. *Onderstepoort Journal of Veterinary Research* **63**: 65–90.
MORTON, J.F. 1994. Lantana, or red sage (*Lantana camara* L., [Verbenaceae]), notorious weed and popular garden flower; some cases of poisoning in Florida. *Economic Botany* **48**: 259–270.
MUNIR, A.A. 1996. A taxonomic review of *Lantana camara* L. and *L. montevidensis* (Spreng.) Briq. (Verbenaceae) in Australia. *Journal of the Adelaide Botanical Gardens* **17**: 1–27.
NESER, S. & CILLIERS, C.J. 1990. Work towards biological control of *Lantana camara:* perspectives. In: Delfosse, E.S. (Ed.) *Proceedings of the Seventh International Symposium on Biological Control of Weeds.* 363–369. Istituto Sperimentale per la Patologia Vegetale Ministero dell'Agricoltura e delle Foreste, Rome.
OOSTHUIZEN, M.J. 1964. The biological control of *Lantana camara* L. in Natal. *Journal of the Entomological Society of Southern Africa* **27**: 3–16.
PALMER, W.A. & PULLEN, K.R. 1995. The phytophagous arthropods associated with *Lantana camara, L. hirsuta, L. urticifolia* and *L. urticoides* (Verbenaceae) in North America. *Biological Control* **5**: 54–72.
PALMER, W.A., WILLSON, B.W. & PULLEN, K.R. 1996. The host range of *Aconophora compressa* Walker (Homoptera: Membracidae): a potential biological control agent for *Lantana camara* L. (Verbenaceae). *Proceedings of the Entomological Society of Washington* **98**: 617–624.
PALMER, W.A. & PULLEN, K.R. 1998. The host range of *Falconia intermedia* (Distant) (Hemiptera: Miridae): a potential biological control agent for *Lantana camara* L. (Verbenaceae). *Proceedings of the Entomological Society of Washington* **100**: 633–635.
PERKINS, R.C.L. & SWEZEY, O.H. 1924. The introduction into Hawaii of insects that attack lantana. *Hawaii Sugar Planters Association Experimental Station Bulletin (Entomological Series)* **16**: 1–83.
RADUNZ, L.A.J. 1971. Some aspects of the preferential behaviour of *Teleonemia scrupulosa* Stål, towards its host plant *Lantana camara.* Hons. thesis, University of Queensland.
SAVINI, V. 1997. Evaluación de los datos sobre los phytophaga dañinos en Venezuela (Coleoptera). *Boletin de Entomologia Venezolana* (Serie Monografias) **1**: 95–96.
SMITH, L.S. & SMITH, D.A. 1982. The naturalised *Lantana camara* complex in eastern Australia. *Queensland Botanical Bulletin No. 1.* Queensland Department of Primary Industry, Brisbane.
SPIES, J.J. 1984. A cytotaxonomic study of *Lantana camara* (Verbenaceae) from South Africa. *South African Journal of Botany* **3**: 231–250.
SPIES, J.J. & DU PLESSIS, H. 1987. Sterile *Lantana camara:* fact or theory. *South African Journal of Plant and Soil* **4**: 171–174.
SPIES, J.J. & STIRTON, C.H. 1982a. Chromosome numbers of South African plants. *South African Journal of Botany* **48**: 21–22.
SPIES, J.J. & STIRTON, C.H. 1982b. Meiotic studies of some South African cultivars of *Lantana camara*

(Verbenaceae). *Bothalia* **14**: 101–111.
SPIES, J.J. & STIRTON, C.H. 1982c. Embryo sac development in some South African cultivars of *Lantana camara*. *Bothalia* **14**: 113–117.
STEGMAIER, C.E. 1966. A leaf miner on *Lantana* in Florida, *Ophiomyia camarae* (Diptera, Agromyzidae). *The Florida Entomologist* **49**: 151–152.
STIRTON, C.H. 1977. Some thoughts on the polyploid complex *Lantana camara* L. (Verbenaceae). *Proceedings of the Second National Weeds Conference of South Africa*. 321–344. A.A. Balkema, Cape Town.
SWARBRICK, J.T., WILLSON, B.W. & HANNAN-JONES, M.A. 1995. The biology of Australian weeds: *Lantana camara* L. *Plant Protection Quarterly* **10**: 82–95.
WINDER, J.A. & HARLEY, K.L.S. 1983. Phytophagous insects on lantana in Brazil and their potential for biological control in Australia. *Tropical Pest Management* **29**: 346–362.