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COMMENTARY

Review and Evaluation of Lantana Biocontrol Programs

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This paper provides a review of lantana (*Lantana camara* L.) biological control programs worldwide. Tables on the origins of the agents introduced for the biocontrol of lantana, are presented, including references to the biology and/or host-tests for each species. Establishment and control rates of the introduced agents and cases leading to partial control of lantana are discussed. From the review, feeding groups and species contributing to control were identified. Leaf-, flower-, and fruit-feeding species were the most successful feeding groups, and the leaf-mining chrysomelid, *Uroplata girardi* Pic, was the most successful control agent. The main factor preventing establishment was the number of individuals released, while cultivar preferences, parasitism and predation, and climate reduced control. The implication of these results for lantana biocontrol programs is discussed, and future research requirements are identified. © 2000 Academic Press

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INTRODUCTION

For almost a century, attempts have been made to control *Lantana camara* (L.) using insects (Perkins and Swezey, 1924; Holloway, 1964; Swarbrick *et al.*, 1995). To date, 38 species have been released in 29 countries (Willson, 1993; Swarbrick *et al.*, 1995; Julien and Griffiths, 1998). Despite the amount of research effort and time expended on lantana biological control, results have been variable. Success in several countries led Crawley (1986, 1989a,b) to rate lantana as the "most successful target of weed biocontrol," but he also listed lantana as the most "frequent unsuccessful target" because of failures in many locations. Three leaf-feeding insect species were identified as successful agents, but different species have been successful in different countries (Crawley, 1986, 1989a,b).

Inability to predict success is attributed to the low genetic uniformity of lantana and its ability to colonize diverse habitats (Crawley, 1989a,b; Willson, 1993; Swarbrick *et al.*, 1995). Because of this, Willson (1993) suggested that agent selection procedures proposed by Harris (1973a,b), Goeden (1983), and Wapshere (1985) are irrelevant. Instead, species were prioritized according to their success in other countries or because they were host-specific and added to the folivore complex already introduced (Harley and Kassulke, 1971; Waterhouse and Norris, 1987; Willson, 1993). However, this selection method has failed to achieve successful control, and many countries are introducing new species to maximize lantana suppression (Willson, 1993; Neser, 1994; Palmer and Pullen, 1995; Swarbrick *et al.*, 1995). Because each new species costs 3 to 5 scientist-years in terms of research associated with host-specificity testing, development of mass-rearing techniques, and releases (Waterhouse and Norris, 1987; Harris, 1991), guidelines that improve selection of effective natural enemies are required.

The objective of this paper was to develop selection guidelines based on an analytic review of all lantana biocontrol programs. Waterhouse and Norris (1987) provide the most complete review of lantana programs, but only for Pacific Rim countries. Neser and Cilliers (1989) supply some guidelines, but base their conclusions on the 1982 review of Julien (1982), or papers published before 1987, and did not include statistical analysis of programs. Using a variation of the success rating of Crawley (1989a,b), I analyzed current data on the success of individual lantana agents in controlling lantana in every location of release. The following factors were included in my analyses to identify trends in agent selection or correlations with establishment or control of lantana: *Lantana* taxon from which the biocontrol agent had been collected, insect taxa, part of

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the plant attacked, cultivar preference, number of individuals released, and natural enemies.

Lantana taxon. *Lantana* biocontrol agents have been collected from many different species of *Lantana* under the assumption that coevolutionary history or "old" vs "new" insect–plant associations (Hokkanen and Pimental, 1984) do not affect the likelihood of establishment or control. However, this premise was never tested for lantana.

Insect taxa. Harley (1971), Winder and Harley (1982), and Neser and Cilliers (1989) suggested that Lepidoptera were less likely to control lantana because they usually are heavily parasitized.

Part of the plant attacked. Crawley (1989a,b) identified insects that attacked the leaves as the most successful feeding group. Perkins and Swezey (1924) considered flower- and fruit-feeding species to be the most successful feeding group.

Cultivar preference. Preferences of agents for particular cultivars were thought to limit control (Harley, 1973; Neser and Cilliers, 1989; Swarbrick *et al.*, 1995).

Number of individuals released. Beirne (1985) suggested that the chances of colonization were less than 10% if 5000 or fewer individuals are released.

Natural enemies. Goeden and Louda (1976), Cullen and Snowball (1979), and Crawley (1989a,b) identified natural enemies (predators, parasitoids, disease) as some of the most important factors that limit establishment and control of biological control agents.

These factors are discussed relative to the origin of lantana, the insects surveyed and those introduced for biocontrol, the success of all introduced agents in terms of establishment and control of lantana, the factors that limit establishment and/or control, and the responses of lantana to biocontrol agents. This information was used to derive guidelines for future programs.

ORIGIN OF LANTANA

The specific geographic origin of *L. camara* is unknown. Some authors suggested that *L. camara* is native to South America or Mexico (Howard, 1969; Smith and Smith, 1982; Spies and du Plessis, 1987), while others suggested the West Indies as the site of origin (Moldenke, 1973; Stirton, 1977; Palmer and Pullen, 1995). In the mid-16th and 17th centuries, lantana species, including *L. camara,* were imported into Europe as horticultural plants from the Americas (Stirton, 1977; Swarbrick *et al.*, 1995). Hundreds of cultivars of mixed parentage were created in Europe from this stock (Howard, 1969). These cultivars were transported back to the Americas and to Australia, India, and Africa in the mid-19th century (Table 1; Howard, 1969; Stirton, 1977; Swarbrick, 1985). Many cultivars escaped cultivation and became weeds (Table 1; Spies, 1984; Swarbrick, 1985; Waterhouse and Norris, 1987; Palmer and Pullen, 1995).

Weed scientists often refer to cultivars as *L. camara,* implying that they all belong to one monotypic species. However, reports suggest that cultivars were derived from different lantana species or subspecific taxa (e.g., *Lantana camara aculeata* and *L. camara* var. *mista*) and many are of indeterminate origin (Table 1). Cultivars have been classified according to flower color, presence or absence of thorns, and growth habit (Smith and Smith, 1982). Cultivars differ in their susceptibility to insect attack, chemical constituents, and toxicity to livestock (Smith and Smith, 1982; Neser and Cilliers, 1989; Taylor, 1989; Cilliers and Neser, 1991). In most countries, a pink and yellow flower cultivar is common (Table 1). Scott *et al.* (1997) recently questioned the use of flower color to classify lantana. Their comparison of the most common cultivars in Queensland, Australia, revealed no correlation between flower color and cultivar based on DNA analysis.

CHARACTERISTICS OF INSECTS SELECTED AS BIOCONTROL AGENTS

The insect species surveyed worldwide were compared with those released for lantana biocontrol on the basis of insect order, part of plant attacked, and host specificity. Survey data were obtained from Palmer and Pullen (1995) and Winder and Harley (1983), and data on released insects were from host-testing reports or from Swarbrick *et al.* (1995).

Worldwide Surveys

Potential biological control agents were surveyed in Brazil, Peru, Colombia, and Central and North America (Perkins and Swezey, 1924; Krauss, 1953, 1962; J. Mann, unpublished data, 1954; Harley, 1974; Diatloff, 1977; Winder, 1980; Winder and Harley, 1983; Palmer and Pullen, 1995). Cumulatively, these surveys resulted in the collection of 550 phytophagous insect species from *Lantana* spp. in Central and North America and 345 species from Brazil (Winder and Harley, 1983; Palmer and Pullen, 1995).

Taxa and Host Range

Species were divided with respect to taxonomic groups, plant part attacked, and host specificity (Figs. 1 and 2). Polyphagous species are defined by Harley and Forno (1992) as "insects that feed on many different species of plants." Oligophagous species feed on a single order, family, or genus, while monophagous insects are restricted to a single plant species (Harley and Forno, 1992).

Coleoptera, particularly Chrysomelidae, was the dominant order collected from lantana, followed by

TABLE 1

Country of Introduction and the Number of Weedy Cultivars

Area of introduction	Date of introduction and area of origin	Species	Number of weedy cultivars; most common cultivars	Reference
Australia	?	*L. camara, sensu lato*	29; common pink, pink-edged red	Smith and Smith (1982); Swarbrick (1985); Swarbrick *et al.* (1995)
Fiji	?	*L. camara* L.; *L. aculeata* L.	4–5; common pink, common-pink-edged red, Mt. Berriman pink, undescribed white, Bundaberg large-flowered pink (classification based on Smith and Smith, 1982)	Kamath (1979); B. W. Willson (unpublished data, 1995)
Hawaii (United States of America)	South America	*L. camara* var *mista* L. H. Bailey, *L. camara* var *aculeata* Moldenke	2; Hawaiian orange red, Hawaiian pink	Pemberton (1964)
India	1807	*L. camara* var *aculeata* Moldenke	?; not reported	Muniappan and Viraktamath (1986); Stirton (1977); Thakur *et al.* (1992)
Federated States of Micronesia	?	*L. camara aculeata* Moldenke (pink and yellow flowers); *L. camara* var *mista* L. H. Bailey	4; orange-red and yellow (=Hawaiian orange-red?), pink and yellow flowers, light orange and yellow, like Hawaiian pink but corolla bordered with orange	Denton *et al.* (1991a)
New Caledonia	1861 ?	*L. camara* L.	?; common pink	Gutierrez and Forno (1989); Stirton (1977)
Solomon Islands	?	*L. camara* L.	2; Hawaiian pink, common pink	K. L. S. Harley (unpublished data, 1993)
South Africa	1883 ?	*L. camara, sensu lato*	40+ cultivars; 5 main weedy cultivars; pink, orange/red	Neser and Cilliers (1989); Stirton (1977)
Vanuatu	?	*L. camara* L.	2; common pink, Hawaiian pink	B. W. Willson (unpublished data, 1995)

Note. ?, origin unknown; introduced by European settlers.

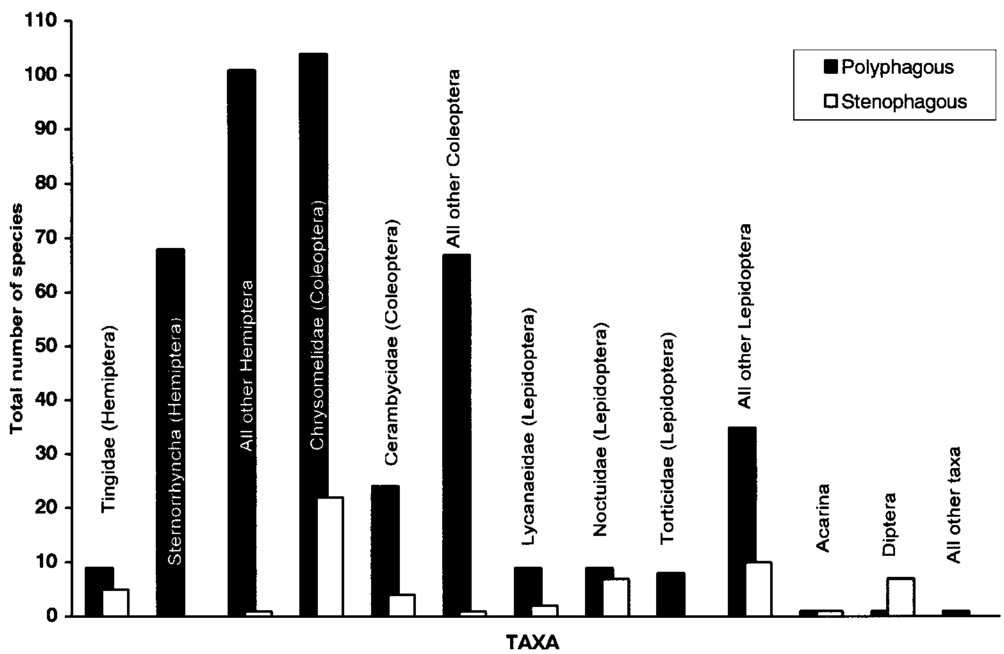

FIG. 1. The number of species of insects and mites recorded on lantana in North America by taxon and host range (Palmer and Pullen, 1995).

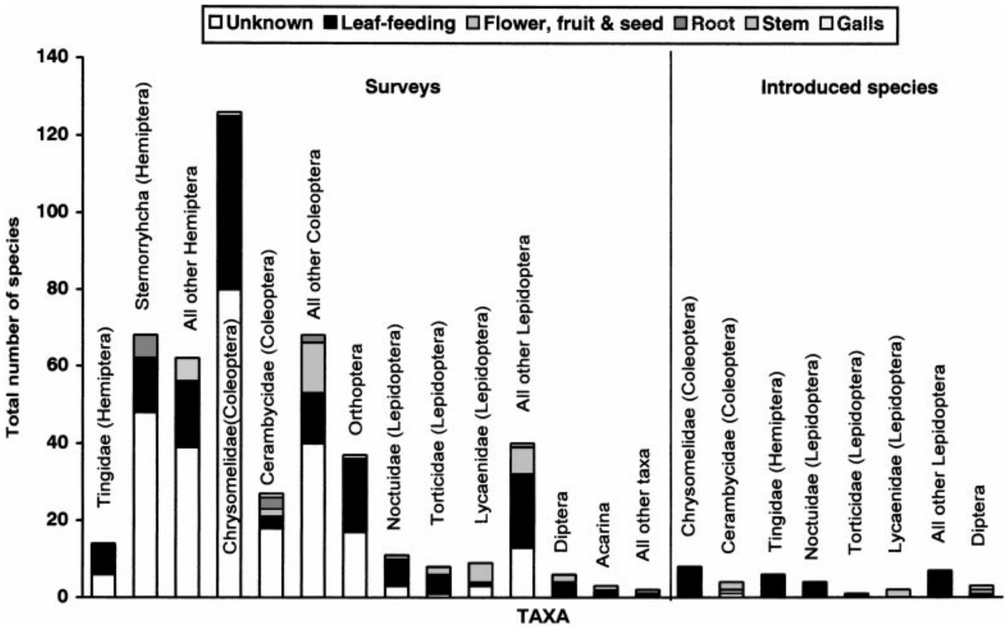

FIG. 2. The number of insect and mite species recorded in surveys on lantana or introduced for biological control of lantana by feeding site and taxon (Winder and Harley, 1982, 1983; Palmer and Pullen, 1995; Swarbrick *et al.*, 1995). Surveys, species collected during foreign explorations for biocontrol agents.

Hemiptera and Lepidoptera (Figs. 1 and 2). Most taxa collected (56%) were polyphagous, or the host range was unknown (Fig. 1; Palmer and Pullen, 1995). Only 5.6% ($n = 26$) of all insect species collected were considered sufficiently specific to be potential agents (i.e., they feed and breed exclusively on *Lantana* species). Diptera (Agromyzidae, Cecidomyiidae, and Tephritidae) were the most host specific insects collected (Fig. 1).

The insect taxa collected during worldwide surveys are reasonably represented among species introduced for lantana biocontrol with three notable exceptions: suborder Sternorrhyncha and orders Orthoptera and Acarina. These taxa were not considered for introduction because most of their constituent species are polyphagous (Figs. 1 and 2; Palmer and Pullen, 1995).

Feeding Habits

The feeding habits of 49% of all species collected in North America were unknown (Palmer and Pullen, 1995). Data from Brazil are not reported here because little information was provided on feeding habits for individual species, and some species overlapped with those collected in North America (Winder and Harley, 1983; Palmer and Pullen, 1995). Of the 51% of species with known feeding habits collected in North America, leaf-feeding insects (e.g., sucking, mining, and chewing) composed 29%, flower- or fruit-feeders constituted 7.5%, and stem- or root-boring species composed 2.5% (Fig. 2). These feeding groups were similarly represented among the species introduced for lantana biocontrol: the majority were leaf-feeders (66%; $n = 25$ species), 18% were flower- or fruit-feeding insects ($n = 7$ species), and 13% were stem- or root-borers ($n = 5$ species) (Fig. 2). This suggests that the selection of agents was based on availability rather than feeding group. The exception is the group of stem- and root-boring species, which is overrepresented in introductions compared to surveys. Although my conclusions on agent selection agree with those of Winder (1980), other factors such as ease of rearing, ease of transport, and survivability may have influenced agent selection. With the exception of the Cerambycidae (discussed under "*Factors Preventing Establishment*"), these factors could not be extracted from the literature.

SUCCESS OF INSECTS INTRODUCED FOR LANTANA BIOCONTROL

Introduction of a species to a country was regarded as an individual case, and each case was given an overall success score (see "*Success Score*"). Data were obtained from published and unpublished literature and the review by Julien and Griffiths (1998). The terms used to describe the effects of insects varied enormously in the literature. For example, the terms "little effect," "partial control," "minimal control," and "no effect" were used to describe the outcomes of unsuccessful projects. I reinterpreted these descriptions based on Crawley's (1989a,b) and Crutwell-McFadyen's (1998) definitions of successful control (Table 2). Given the type of data available, the criteria that I employed were necessarily subjective.

TABLE 2

Success Ratings Used in the Evaluation of Individual Insect Species on a Per Country Basis

Rating	Established	Rating	Control
0	Not established, status unknown, or temporarily established but the population perished	0	Not effective, no control, no marked effect, effects unknown, or status unknown
50	Established at 1–3 sites, poorly established	0.1	Little effect, limited control, contributes to control
75	Moderate establishment	0.5	Moderate control, partial control, highly damaging but is limited in its effectiveness by parasites or climate
100	Widely established, well established	0.9	Highly damaging to lantana, highly effective
	N/A	1.0	Successful control, complete control, weed no longer considered to be a problem

Note. Some examples of comments on establishment and effectiveness were taken from contributors to Julien and Griffiths (1998); my rating in left column.

Success Score

Crawley (1989a,b) outlined a quantitative approach to analysis using the area of infestation reduced by a biocontrol agent as a measure of success. Unfortunately, these types of data were not available for any lantana biocontrol program. I used Crawley's (1989a) simple system, rating the success of a species by the degree of control achieved, with a scale of 0 to 1, and added another category, establishment, as an indication of the extent of the geographical range of lantana over which the biocontrol agent exerted its effect (Table 2). Each species in every country in which it was introduced (a case) was assigned a rating in both categories. These ratings were combined to obtain an overall success score: *Success score = establishment rating × effectiveness rating.* Success scores can range from 0 (not established and/or not effective) to 100 (widely established, complete control of lantana achieved). For each species, the percentage of successful cases of control was obtained by dividing the total number of cases with a success score of 45–100 by the total number of releases.

Results

The success ratings of all releases, their areas of origin, their host lantana species, and references providing details of distribution, host testing, biology, or a description of each species are listed in Table 3. The data presented in Table 3 extend those of Julien and Griffiths (1998) to include species that were imported but not released.

One species, the noctuid *Hypena laceratalis* Walker, was identified by Common (1957) as a native Australian species. This species was also endemic to South Africa and Asia (Cilliers and Neser, 1991; Julien and Griffiths, 1998). The native host(s) of this species are unknown (Common, 1957; Cilliers and Neser, 1991).

(a) Lantana taxa. In addition to *L. camara*, insects were collected from *L. glutinosa* (Poeppig), *L. hispida* (=*L. hirsuta* Martius and Gal.), *L. tiliaefolia* (Chamisso), *L. urticifolia* (Miller), and *L. urticoides* (Hayek) (Winder, 1980; Winder and Harley, 1983; Palmer and Pullen, 1995). Twenty insect species, established in at least one country, were collected from *L. camara* and other *Lantana* species (Table 3). No relationship existed between host *Lantana* species in the country of origin and proportion of agents that became established ($\chi^2 = 8.36$, $df = 1$, $P > 0.1$). The practice of collecting agents from different lantana species (i.e., new associations) appears valid. Analysis of feeding groups and likelihood of establishment was significant ($\chi^2 = 25.62$, $df = 1$, $P > 0.01$). There were no significant differences between taxa in success of establishment (Pearson's correlation coefficient = 0.03, $P = 0.85$, $n = 38$; Table 3).

(b) Host specificity. Most of the introduced agents were host-specific. Host-specificity testing of *Teleonemia scrupulosa* (Stål), *Leptobyrsa decora* (Drake), and *Plagiohammis spinipennis* (Thomson) suggested that they could feed on teak (*Tectona grandis* L., Verbenaceae), sesame (*Sesasum indicum* L., Pedaliaceae), and species in three other families (Harley and Kunimoto, 1969; Harley and Kassulke, 1971). On one occasion, *T. scrupulosa* was recorded feeding on sesame in East Africa (Davies and Greathead, 1967; Greathead, 1968). The chrysomelids *O. scabripennis* and *U. girardi* occasionally fed on mint (*Mentha* species L.) and basil (*Ocimum basilicum* L.) (Labiateae) (Harley, 1969b), and adult *O. scabripennis* were observed feeding on a species of native Australian shrub, *Clerodendrum floribundum* L. (Verbenaceae) (D. P. A. Sands, CSIRO, pers. comm., 1998).

Two accidentally introduced species, *Orthezia insignis* (Browne) and *Phenacoccus parvus* (Morrison), were highly damaging to lantana (Table 3). The scale insect *O. insignis* was first recorded in Hawaii in 1899 and India in 1915 (Perkins and Swezey, 1924; Davis *et al.*, 1992; Julien and Griffiths, 1998; Table 4). Because *O. insignis* infests other cultivated ornamentals, its use by cattle ranchers in Hawaii was discouraged (Davis *et al.*, 1992). The mealybug, *Phenacoccus parvus* (Morrison), first noted in southeast Queensland in 1988 (Swarbrick and Donaldson, 1991), is considered a threat to economically important crops (Swarbrick and Donaldson, 1991). However, Marohasy (1994, 1997, 1998) suggests that *P. parvus* is unlikely to become a pest, based on laboratory and field studies and an examination of host records.

(c) Country of origin. Nine (45%) of the successfully established species came from Mexico ($n = 9$) and 38% of all importations were obtained from colonies in Hawaii that had originated in Mexico ($n = 76$) (Julien and Griffiths, 1998). This result was not surprising because, before 1970, programs were based on the importation of species considered successful in Hawaii (Julien and Griffiths, 1998). Since 1970, Australian scientists actively surveyed, tested, and released new species collected from Brazil, Mexico, and other countries in North America (Winder and Harley, 1983; Palmer and Pullen, 1995; Swarbrick *et al.*, 1995). Lower rates of establishment were associated with these species (e.g., *Octotoma*, *Uroplata*, and *Teleonemia* spp.; Table 3) because they were often released without prior knowledge of the likelihood of establishment or control.

(d) Successes achieved. Although complete control of lantana has not occurred, partial control of lantana has been achieved in 13 localities with nine species (Table 4). Seventeen cases (68%) involved leaf-feeding, mining, or sucking insects; 7 (28%) cases involved flower- or fruit-feeders; 1 case involved a stem-borer (4%) (Table 4). Most cases were reported in Hawaii with 6 species (mostly flower-feeding Lepidoptera) introduced by either Koebele or Krauss and Mann before 1960 (Davis *et al.*, 1992; Table 4). The leaf-mining chrysomelid *U. girardi* was the single most successful species, achieving partial control of lantana in 7 localities (Table 4).

Crawley (1989a,b) attributed 31% of successful cases of control to the tingid *T. scrupulosa*, compared with 24% (six cases of partial control) in this analysis (Table 4). Crawley's (1989a) three successful species were included in my list (Table 4), but the percentages of cases leading to success were considerably different. These discrepancies are probably due to the incorporation of more recent data in my analysis (after 1989). For example, *U. girardi* was not included in Crawley's list of successful species (Crawley 1989a,b). This species has only been reported as a successful agent since 1987–1998 (Table 4).

FACTORS INFLUENCING ESTABLISHMENT AND CONTROL OF LANTANA

Using the database from the previous section, I incorporated information on whether insect numbers, parasitism and predation, climate, and mass-rearing problems had influenced establishment and control. Data were obtained from published and unpublished literature and the review by Julien and Griffiths (1998). Factors that influenced establishment and control are presented in Fig. 3. The thickness of the arrow indicates the importance of each factor; percentages (based on the total number of cases) are also shown. The most important factor influencing establishment was the number of individuals released, while climate and parasitism/predation reduced control (Fig. 3). These factors may have been overestimated because few authors provided details of how the factor influenced control. For example, parasitism and predation were cited in 14 cases, but apart from identifying the species of parasitoid or predator found, there were no details of parasitism rates or experiments to determine how populations were affected.

Factors Preventing Establishment

Low numbers of individuals released in an introduction attempt account for 23.6% of all cases of failure (13 cases) (Fig. 3). Most cases were associated with Coleoptera (Cerambycidae, 1 case; Hispinidae, 5 cases) or Lepidoptera (8 cases); Hemiptera accounted for 1 case. Beirne (1985) suggested that the chances of colonization are less than 10% if 5000 or fewer individuals are released. In 8 cases, fewer than 300 individuals were released (Cilliers, 1983; Fullaway, 1956; Julien and Griffiths, 1998; Kamath, 1979; O'Connor, 1960).

Four cases (7.3%) were affected by rearing problems. The mirid *Adfalconia intermedia* (Distant), could not be reared because the neonate bugs failed to feed, dying as first instars. Willson (1993) and Palmer and Pullen (1998) attributed this to cultivar differences. The cerambycid *P. spinipennis* proved difficult to rear in Australia, Hawaii, Fiji, and India (Harley and Willson, 1968; Kamath, 1979; Thakur *et al.*, 1992). Harley and Willson (1968) reported that 7–46% of *P. spinipennis* larvae died during rearing. Though they developed an artificial diet, reducing mass-reared larval mortality to 4% (Harley and Willson, 1968), the species became established at only one site in Australia. In Fiji, the cerambycid *Aerenicopsis championi* Bates was difficult to rear and the project was abandoned (O'Connor, 1960). In South Africa, problems with mass-rearing the leaf-rolling moth, *Salbia haemorrhoidalis* Guenée, culminated in the release of 114 individuals (Cilliers and Neser, 1991). Though *S. haemorrhoidalis* became established, it is not effective (Cilliers and Neser, 1991).

In one case (1.8%), problems with the host plant affected the establishment of *P. spinipennis*. In Australia, *P. spinipennis* became established at one site in New South Wales (Winder and Harley, 1983; Taylor, 1989; Swarbrick *et al.*, 1995). At other sites, failure to

TABLE 3

Insects Introduced for the Biological Control of Lantana, Including Host Species and References to the Biology, Distribution, and/or Host-Testing Results

Species author (Order: Family)	Area of origin	Host *Lantana* species in country of origin	R	E	A	C	References/comments
		Root-feeding insects					
Langsdorfia franckii Hübner* (Lepidoptera: Cossidae)	Mexico	*L. camara*	1	0	0	0	Perkins and Swezey (1924)
Parevander xanthomelas Guérin-Méneville (=*Evander xanthomelas* Guérin-Méneville and *P. hoverei* Giesbert) (Coleoptera: Cerambycidae)	Mexico	*L. camara*	1	0	0	0	Perkins and Swezey (1924); Giesbert and Penrose (1984)
		Gall-forming insects					
Eutreta xanthochaeta Aldrich (=*Eutreta sparsa* Aldrich) (Diptera: Tephritidae)	Mexico	*L. camara, L. urticifolia*	3	1	0	0	Aldrich (1923); Perkins and Swezey (1924); Palmer and Pullen (1995)
		Stem-boring insects					
Aerenicopsis championi Bates[N] (Coleoptera: Cerambycidae)	Mexico	*L. camara; L. urticifolia; L. hispida*	2	1	0	0	Krauss (1962); B. W. Wilson (unpublished data, 1994)
Hepialus sp. (Lepidoptera: Hepialidae)	Mexico	*Lantana* sp.	1	0	0	0	Perkins and Swezey (1924)
Plagiohammis spinipennis Thomson (Coleoptera: Cerambycidae)	Colombia, Costa Rica, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela	*L. camara; L. hirsuta*	5	2	0	1	Harley and Willson (1968); Harley (1969a); Harley and Kunimoto (1969); Palmer and Pullen (1995)
		Flower- and fruit-feeding insects					
Apion species A (Coleoptera: Apionidae)	Mexico	*L. tiliaefolia*	1	0	0	0	Perkins and Swezey (1924)
Apion species B (Coleoptera: Apionidae)	Mexico	*L. tiliaefolia*	1	0	0	0	Perkins and Swezey (1924)
Epinotia lantana Busck (=*Crocidosema lantana* Busck) (Lepidoptera: Tortricidae)	Mexico	*L. camara; L. hispida; L. urticifolia*	4	4	4	3	Common (1957); Waterhouse and Norris (1987)
Lantanophaga pusillidactyla Walker (=*Platyptilia pusillidactyla* Walker) (Lepidoptera: Pyralidae)	Mexico	*L. camara; L. hispida*	7	5	4	2	Rao (1920); Waterhouse and Norris (1987); Palmer and Pullen (1995)
Ophiomyia lantanae Froggatt (=*Agromyza lantanae* Froggatt) (Diptera: Agromyzidae)	Mexico	*L. camara*	11	9	16	1	Perkins and Swezey (1924); Cilliers (1987a); Spencer (1990)
Tmolus sp. (*echion* group) (Lepidoptera: Lycaenidae)	Mexico	*L. camara*	2	1	0	0	Perkins and Swezey (1924); Palmer and Pullen (1995)
Strymon bazochii (Godart) (=*Thecla bazochii* (Godart) (Lepidoptera: Lycaenidae)	Mexico	*L. camara; L. hispida; L. urticifolia*	3	2	0	0	Perkins and Swezey (1924); Palmer and Pullen (1995)
		Leaf- and stem-sucking insects					
Aconophora compressa (Walker)[N] (Hemiptera: Membracidae)	Mexico	*L. hispida*	1	0	0	0	Palmer *et al.* (1996)
Falconia Intermedia (Distant)* (Hemiptera: Miridae)	Mexico, North America	*L. hispida*	—	—	—	—	Swarbrick *et al.* (1995); Palmer and Pullen (1998)
Alagoasa parana Samuelson (Coleoptera: Chrysomelidae)	Brazil	*L. glutinosa; L. tiliaefolia*	2	0	0	0	Winder *et al.* (1988)
Leptobyrsa decora Drake (Hemiptera: Tingidae)	Colombia, Ecuador, Peru	*Lantana* sp.	9	2	1	0	Harley and Kassulke (1971); Melksham (1984)
Orthezia insignis Browne (Hemiptera: Ortheziidae)	Sri Lanka	Unknown	1	1	4	1	Perkins and Swezey (1924); Davis *et al.* (1992)
Teleonemia bifasciata Champion (Hemiptera: Tingidae)	Brazil	Unknown	1	0	0	0	Julien and Griffiths (1998); generally referred to as *Teleonemia* sp.
Teleonemia elata Drake (Hemiptera: Tingidae)	Brazil, Chile, Paraguay, Peru	*L. glutinosa; L. tiliaefolia*	5	0	0	0	Harley and Kassulke (1971)
Teleonemia harleyi Froeschner (Hemiptera: Tingidae)	Mexico	*Lantana* sp	1	1	0	0	Froeschner (1970); Harley and Kassulke (1971); Baars (1997)

TABLE 3—*Continued*

Species author (Order: Family)	Area of origin	Host *Lantana* species in country of origin	R	E	A	C	References/comments
		Leaf- and stem-sucking insects—*Continued*					
Teleonemia prolixa Stål (Hemiptera: Tingidae)	Mexico	*L. glutinosa; L. tiliaefolia*	1	0	0	0	Harley and Kassulke (1971)
Teleonemia scrupulosa (Stål) (=*T. vanduzei* Drake; *T. lantanae* Distant) (Hemiptera: Tingidae)	Mexico, Texas, Florida, Brazil, Chile, Paraguay, Venezuela	*L. camara; L. hispida; L. urticifolia; L. urticoides*	27	25	4	4	Perkins and Swezey (1924); Simmonds (1929); Harley and Kassulke (1971); Cilliers (1987a)
Teleonemia validicornis Stål (Hemiptera: Tingidae)	Colombia, Surinam, French Guiana, Guyana, Brazil, Argentina, Venezuela, Panama, Curaçao	*L. camara*	—	—	—	—	Harley and Kassulke (1971)
		Leaf-chewing or leaf-mining insects					
Autoplusia illustrata Guenée (Lepidoptera: Noctuidae)	Mexico, Colombia	*L. camara*	2	0	0	0	—
Calycomyza lantanae Frick (=*Phytobia lantanae* Frick) (Diptera: Agromyzidae)	Mexico, Peru, Trinidad	*L. camara*	5	5	8	1	Harley and Kassulke (1974); Spencer (1990)
Charidotis pygmaea (Coleoptera: Chrysomelidae)	Brazil, Argentina	*L. camara; L. montevidensis*	2	0	0	0	Swarbrick *et al.* (1995)
Cremastobombycia lantanella Busck (Lepidoptera: Gracillariidae)	Mexico, south Texas	*L. camara; L. hispida L. urticofolia; L. urticoides*	1	1	0	1	Perkins and Swezey (1924); Perkins (1966)
Diastema tigris Guenée (Lepidoptera: Noctuidae)	Panama, Trinidad, Mexico	*L. urticifolia*	10	1	0	0	Cilliers and Neser (1991); Palmer and Pullen (1995)
Ectaga garcia Becker (Lepidoptera: Depressariidae)	Mexico	*L. camara; L. montevidensis*	1	0	0	0	Swarbrick *et al.* (1995)
Hypena laceratalis Walker [=*Hypena strigata* (Fabricius) and *Hypena jussalis* (Walker)] (Lepidoptera: Noctuidae)	Africa, Indo-Malaysia, Australia	*L. camara*	8	8	1	2	Perkins (1966); Waterhouse and Norris (1987); indigenous to Australia, Africa, and the Philippines
Neogalea sunia (Guenée) [=*Catabena esula* (Druce) and *Neogalea esula* (Druce)] (Lepidoptera: Noctuidae)	Mexico	*L. camara; L. urticifolia; L. urticoides*	5	3	1	1	Harley (1973); Waterhouse and Norris (1987)
Octotoma championi Baly (Coleoptera: Chrysomelidae)	Costa Rica, Guatemala, Mexico, Texas	*L. camara; L. hispida; L. urticifolia*	3	1	0	0	Krauss (1964); Diatloff (1977); Riley and Balsbaugh (1988)
Octotoma plicatula (Fabricius) [=*O. gundlachi* (Suffrain)?] (Coleoptera: Chrysomelidae)	Cuba, Brazil, Honduras, eastern USA	*Lantana* spp.	1	0	0	0	Krauss (1962); Riley and Balsbaugh (1988); Davis *et al.* (1992)
Octotoma scabripennis Guérin-Méneville (Coleoptera: Chrysomelidae)	Mexico	*L. camara; L. glutinosa*	11	6	0	3	Krauss (1964); Harley (1969b); Cilliers (1987a)
Pseudopyrausta santatalis (Barnes & McDunnough) [=*Pseudopyrausta acutangulalis* (Snellen) or *Blepharomastix acutangulalis* (Snellen)] (Lepidoptera: Pyralidae)	Mexico, Colombia, Venezuela	*L. camara; L. urticifolia*	3	0	0	0	K. L. S. Harley (unpublished data, 1956); J. Mann (unpublished data, 1954)
Salbia haemorrhoidalis Guenée [=*Syngamia haemorrhoidalis* (Guenée) or *Anania haemorrhoidalis* (Guenée)] (Lepidoptera: Pyralidae)	Mexico	*L. camara; L. hirsuta; L. urticifolia*	13	8	0	1	Waterhouse and Norris (1987); J. Mann (unpublished data, 1954)
Uroplata fulvopustulata Baly [=*Uroplata* sp. (Chapuis) nr *bilineata*] (Coleoptera: Chrysomelidae)	Brazil, Costa Rica, Guatemala, Mexico, Panama, Venezuela	*L. camara; L. urticifolia*	3	1	0	0	Krauss (1964)
Uroplata giradi Pic (Coleoptera: Chrysomelidae)	Brazil, Paraguay, Argentina	*L. camara*	25	23	1	8	Krauss (1964); Harley (1969b); Cilliers (1987a)
Uroplata lantanae Buzzi & Winder (Coleoptera: Chrysomelidae)	Mexico	*Lantana* sp.	2	0	0	0	Winder *et al.* (1984)

Note. Data Extend those of Julien and Griffiths (1998). R, number of releases; E, number of releases resulting in establishment; A, accidental introductions; C, number of cases resulting in partial control of *Lantana* (score ≥45); *, species imported but never released due to rearing difficulties; ^{N}, new species released in Australia or South Africa.

TABLE 4

Cases Where Moderate or Significant Control of Lantana Has Been Achieved

Species	Part of plant damaged	Country of introduction	Year of release	Reference
Plagiohammis spinipennis (Coleoptera: Cerambycidae)	Stem	Hawaii	1954–1960	Davis *et al.* (1992); Harley (1969a)
Epinotia lantanae (Lepidoptera: Tortricidae)	Flower	Federated States of Micronesia	1948	Denton *et al.* (1991a,b)
		Guam	After 1949	Denton *et al.* (1991a,b); Muniappan *et al.* (1996)
		Northern Mariana Islands	After 1949	Denton *et al.* (1991a,b); Julien and Griffiths (1998)
Lantanophaga pusillidactyla (Lepidoptera: Pyralidae)	Flower	Federated States of Micronesia	1948	Denton *et al.* (1991a,b)
		Guam	After 1949	Denton *et al.* (1991a,b); Muniappan *et al.* (1996)
		Palau	After 1949	Denton *et al.* (1991a,b)
Hypena laceratalis (Lepidoptera: Noctuidae)	Leaf	Hawaii	1957	Davis and Krauss (1962a)
			1964	
		Mauritius	1967	Julien and Griffiths (1998)
Neogalea sunia (Lepidoptera: Noctuidae)	Leaf	Hawaii	1955	Davis and Krauss (1962a,b); Davis *et al.* (1992)
Octotoma scabripennis (Coleoptera: Chrysomelidae)	Leaf	Hawaii	1902; 1954	Davis and Krauss (1962a,b); Davis *et al.* (1992)
Uroplata girardi (Coleoptera: Chrysomelidae)	Leaf	Fiji	1969	K. L. S. Harley (unpublished data, 1993); Julien and Griffiths (1998)
		Hawaii	1961	Davis *et al.* (1992)
		Northern Mariana Islands	1963; 1967	Denton *et al.* (1991a,b); Muniappan *et al.* (1996)
		New Caledonia	1977	Gutierrez and Forno (1989)
		Solomon Islands	1993	Anon. (1993); Julien and Griffiths (1998)
		South Africa	1974–1984	Cilliers (1987a,b)
		Tonga Island	1969	Rao *et al.* (1971); Julien and Griffiths (1998)
Salbia haemorrhoidalis (Lepidoptera: Pyralidae)	Flower	Hawaii	1956	Davis *et al.* (1992)
Teleonemia scrupulosa (Hemiptera: Tingidae)	Leaf	Ascension Island	Approx 1973	Julien and Griffiths (1998)
		Australia	1935; 1969–1972	Swarbrick *et al.* (1995)
		Federated States of Micronesia	1948	Denton *et al.* (1991a,b)
		Hawaii	1902; 1952	Davis *et al.* (1992)
		India	1941; 1975–1976	Thakur *et al.* (1992)
		St. Helena	1971	Julien and Griffiths (1998)

Note. In all cases, total score ≥45 (species established at one or more sites and partial control achieved to species widely established and highly damaging to lantana).

become established was attributed to the formation of callus tissue, which was produced in response to stem girdling by the larvae. This killed the larvae before they entered the xylem tissue (Willson, 1974). In Hawaii, an unidentified fungus was associated with the lantana on which *P. spinipennis* became established (Swarbrick *et al.*, 1995). This pathogen rendered the stem soft and spongy, and the absence of this fungus in other countries may account for its failure to become established (Swarbrick *et al.*, 1995).

Factors Inhibiting Control

In 25.5% ($n = 14$) of all cases, predation and parasitism reduced the effectiveness of eight species. Lepidoptera were reported to be parasitized more often than other taxa (6 cases). Six species, *E. lantana*, *S. bazochii*, *Tmolus* sp., *H. laceratalis*, *N. sunia*, and *S. haemorrhoidalis*, were attacked by various parasitic Hymenoptera in Australia, Ghana, Hawaii, South Africa, and Uganda (Perkins, 1966; Taylor, 1989; Cilliers and Neser, 1991; Davis *et al.*, 1992). Parasitoids included native and introduced Hymenoptera (Bethylidae, Braconidae, Ichneumonidae, Eulophidae, and Trichogrammatidae), which attack eggs, larvae, or pupae.

The spectacular control of lantana in Hawaii by the Lepidoptera species *H. laceratalis*, *S. haemorrhoidalis*, and *E. lantana* declined by 1969 (Davis *et al.*, 1992). The decline in effectiveness was thought to be due to

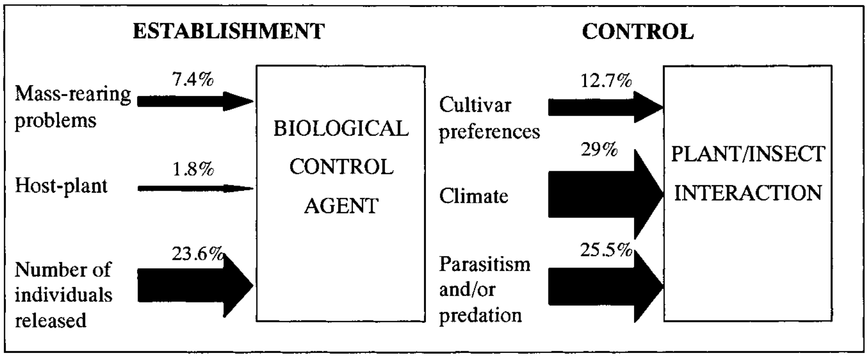

FIG. 3. Diagram showing the importance of various factors on the establishment of introduced biocontrol agents and their effect on lantana (total of 55 cases).

unfavorable weather conditions or parasitism (Davis *et al.*, 1992). However, the reasons for the decline are not known and have never been studied. This level of control is unlikely to be repeated in other countries, as native and introduced parasitoids have broadened their host ranges to include introduced Lepidoptera (Cilliers and Neser, 1991; Swarbrick *et al.*, 1995).

In India, the mymarid wasp, *Erythmelus teleonemiae* Subba Rao, parasitized up to 85% of *T. scrupulosa* eggs (Jayanth and Visalakshy, 1992), and a fungus, *Hirsutella* sp. Patouillard, affects *T. scrupulosa* populations in Australia and Fiji (Simmonds, 1929; Harley, 1973). An eulophid ectoparasitoid of a native chrysomelid, *Notosocantha dorsalis* Waterhouse, was recorded from larvae of *O. scabripennis* and *U. girardi* in Australia (Broughton, 1999a). Unidentified eulophids also parasitize the larvae of *O. scabripennis* and *U. girardi* in Ghana and South Africa (Scheibelreiter, 1980; Cilliers, 1982, 1987a). Generalist predators such as spiders (primarily Thomisidae), birds, neuropteran larvae, predatory bugs, and ants attack tingids (*T. scrupulosa* and *L. decora*) and chrysomelids (*U. girardi* and *O. scabripennis*) in several countries (Simmonds, 1929; Fyfe, 1937; Scheibelreiter, 1980; Liddy, 1982, 1985; Taylor, 1989).

Climate and elevation were implicated directly and indirectly (by their effects on the host plant) in 29% of all cases analyzed (16 cases). For example, the tingid *T. scrupulosa* damaged lantana in dry areas and during dry seasons, but populations were smaller during periods of heavy rainfall and at high elevations (Greathead, 1968, 1971a,b; Livingstone *et al.*, 1981; Davis *et al.*, 1992; Denton *et al.*, 1991a,b; Manian and Udaiyan, 1992; Thakur *et al.*, 1992). Other species affected by climate and elevation include *C. lantanae, L. decora, O. scabripennis,* and *U. girardi* (Cilliers and Neser, 1991; Swarbrick *et al.*, 1995). For these reasons, additional cool-adapted populations of *T. scrupulosa* were imported into Australia and South Africa, and a cool-climate biotype of *U. girardi* was imported into Australia (Taylor, 1989). The fate of these populations is unknown (Taylor, 1989; Cilliers and Neser, 1991).

Cultivar preferences were implicated in only 12.7% ($n = 7$) of all cases but were cited as the main cause of failure of lantana biocontrol programs (e.g., Harley *et al.*, 1979; Cilliers, 1982, 1987a,b; Neser and Cilliers, 1989; Crawley, 1989a,b). In particular, *T. scrupulosa* effectiveness is reduced by its preference for certain cultivars in Australia, Fiji, Guam, Hawaii, Micronesia, South Africa, and Vanuatu (Harley, 1971; Denton *et al.*, 1991b; Neser and Cilliers, 1989; K. L. S. Harley, unpublished data, 1993). Other species reported to display cultivar preferences include *C. lantanae, O. scabripennis,* and *U. girardi* (Radunz, 1971; Harley and Kassulke, 1974; Cilliers, 1982, 1987a,b; Neser and Cilliers, 1989; Taylor, 1989; Cilliers and Neser, 1991; Swarbrick *et al.*, 1995). In these countries, it may be inferred that these agents attacked susceptible cultivars, avoiding those that are more resistant. However, the research conducted to date neither supported nor rejected claims of cultivar preference (Radunz, 1971; Harley *et al.*, 1979; Cilliers, 1982, 1989b). For example, Harley *et al.* (1979) support claims of cultivar preference but draw their conclusions from observations rather than experiments.

A reanalysis of Radunz' (1971) data showed that there were no feeding or ovipositional cultivar preferences for *T. scrupulosa* (B. Congdon, Centre for Tropical Pest Management, pers. comm., 1996). This was supported by experiments with *T. scrupulosa* reared on different flowering cultivars in Brisbane, Australia (B. Congdon and H. Gu, Centre for Tropical Pest Management, pers. comm., 1996). Similarly, field studies of five species of leaf-feeding insects in southeast Queensland, including *T. scrupulosa, C. lantanae, U. girardi,* and *O. scabripennis,* showed that there were no cultivar preferences (Broughton, 1999a). DNA analysis of the most common cultivars occurring in Queensland, Australia, has also shown that there is no correlation between flower color and cultivar (Scott *et al.*, 1997).

PLANT RESPONSES TO INTRODUCED AGENTS

Partial control of lantana was achieved most often with leaf-feeding and fruit- and flower-feeding insects. Five studies examined the impact of some of these agents on lantana. Research in Australia (Harley *et al.*, 1979; Broughton, 1999a) and South Africa (Cilliers, 1982, 1987b) focused on the leaf-feeding species *U. girardi, O. scabripennis,* and *T. scrupulosa*. Muniappan *et al.* (1996) studied the effects of *U. girardi, C. lantanae,* and *H. strigata* in Guam. Winder (1980) carried out the only study within the native range of the weed. Methods included surveys (Harley *et al.*, 1979; Winder, 1980; Cilliers, 1982, 1987b; Muniappan *et al.*, 1996; Broughton, 1999a), insecticide exclusion of agents (Harley *et al.*, 1979; Winder, 1980; Cilliers, 1982, 1987b), and artificial defoliation experiments (Winder, 1980; Winder and van Emden, 1980; Broughton, 1999a).

Effect on Leaves

Surveys and experiments showed that *O. scabripennis, U. girardi,* and *T. scrupulosa* increased defoliation by 10–70% compared to control plants (Harley *et al.*, 1979; Cilliers, 1982, 1987b). This affected the plant by reducing the available leaf area and thus reducing growth rates (Winder, 1980). A reduction in growth rate may reduce the competitive ability and storage reserves of the plant (Forno and Harley, 1977; Winder, 1980; Neser and Cilliers, 1989; Swarbrick *et al.*, 1995). The impact of insect defoliation on competitive ability or the susceptibility of the plant to drought or frost following insect attack was often implied (e.g., Neser and Cilliers, 1989; Cilliers and Neser, 1991; Swarbrick *et al.*, 1995) but not examined.

None of the defoliating insects inflicted damage throughout the year because their populations declined over autumn (*T. scrupulosa*) or winter (*U. girardi* and *O. scabripennis*) (Harley *et al.*, 1979; Cilliers, 1982, 1987b; Broughton, 1999a). This created a “lag period” in spring, when lantana recovered from the previous season’s damage (Harley *et al.*, 1979; Cilliers, 1982, 1987b; Broughton, 1999a). Artificial defoliation experiments demonstrated that when 100% of lantana leaves were removed every month over a 1- to 2-year period, the plant recovered (Winder, 1980; Broughton, 1999a). Insect feeding is more damaging to lantana than the artificial removal of leaves, but these experiments suggested that lantana compensates for insect defoliation (Winder, 1980; Winder and van Emden, 1980; Broughton, 1999a).

Effect on Fruit Production

Lepidoptera such as *Epinotia lananae* Busck, *Lantanophaga pusillidactyla* Walker, *Strymon* (=*Thecla*) spp. (Godart), and the seed-fly *O. lantanae* damage the flower of fruit (Cilliers, 1982, 1987b; Perkins and Swezey, 1924; Muniappan *et al.*, 1996). Defoliating insects also curtail fruit production by reducing growth rates (Harley *et al.* 1979; Winder, 1980; Cilliers, 1982, 1987b). Muniappan *et al.* (1996) estimated that damage by leaf-feeding (*C. lantanae, H. strigata,* and *U. girardi*) and flower- and fruit-feeding (*E. lantanae, O. lantanae,* and *L. pusillidactyla*) species reduced fruit production by 70.1% in Guam.

Research on the effects of flower- and fruit-feeding insects has focused exclusively on the germination rates of fruit infested by *O. lantanae* (Perkins and Swezey, 1924; Graaff, 1987; Thakur *et al.*, 1992; Muniappan *et al.*, 1996; Broughton, 1999b). Perkins conducted the earliest of these experiments in Hawaii. He found no differences in germination rates between infested and uninfested fruit, but he did not state an exact figure (Perkins and Swezey, 1924). Thakur *et al.* (1992) recorded low rates of germination (0–15%) for both groups in India. Conversely, Graaff (1987) recorded germination rates of 0–42% for fly-infested fruit and 0–73% for uninfested fruit in South Africa. The germination rate of uninfested samples was also low (Graaff, 1987). In Australia, fruit dissections and seed-testing of fruit of different ages suggested that embryos are viable for a short period, regardless of whether the fruit is fly infested (Broughton, 1999b).

Cross-pollination experiments carried out by Spies and du Plessis (1987) with commercial and naturalized lantana cultivars suggested that reproductive problems reduce germination rates. When individuals with uneven chromosome numbers (different ploidy levels) were crossed, low germination rates were recorded. The pollen fertility of the different ploidy levels also differed, ranging between 16 and 83.2% (Spies and du Plessis, 1987). These results suggest that factors other than insect damage influence germination. No studies have examined the impact of seed production on local plant populations or whether recruitment of lantana is seed-limited.

Other Parts of the Plant

The remaining feeding groups include a single species of stem-galling fly, *Eutreta xanthochaeta* Aldrich, established in Hawaii (Davis *et al.*, 1992). Though the effect of damage has not been determined, it is thought to be negligible (Davis *et al.*, 1992). Damage to other parts of the plant such as the stems or roots has not been documented. Harley (1969a) made observations on the biology and life history of *P. spinipennis* in Pahala, Hawaii. Although he observed that plants attacked by *P. spinipennis* were severely damaged, these observations were not quantified.

Future Directions

The use of pathogens as an alternative to insects for the biocontrol of weeds has occurred in the last two decades (e.g., Pimental *et al.*, 1984; Crawley, 1989a,b). The future of lantana biocontrol may similarly lie with pathogens. Five pathogen species (rusts and fungi) have been identified as potential agents (Barreto *et al.*, 1995). The rust *Prospodium tuberculatum* is currently being host-tested (Willson, 1993).

CONCLUSIONS AND GUIDELINES FOR FUTURE PROJECTS

My analysis showed that partial control of lantana was achieved in 12 localities. Hawaii had the highest number of introductions that have contributed to partial control of lantana, most of which occurred before 1960. The species most often associated with partial control was the leaf-mining chrysomelid, *U. girardi* (7 localities). Analysis by feeding group showed that leaf-(mining, sucking, and chewing), flower-, and fruit-feeding insects were the most successful groups. However, new defoliating species (i.e., mining, sucking, and chewing) should not be considered for introduction because studies in Australia, Brazil, Guam, and South Africa demonstrated that lantana withstands insect defoliation. Results from artificial defoliation experiments suggest that lantana survives continual defoliation for at least 1 to 2 consecutive years (Winder, 1980; Broughton, 1999a). However, the effects of plant competition (i.e., intra- and interspecific), drought, and frost on lantana are unknown and need to be determined.

Based on artificial defoliation experiments, stem- and root-boring species are most likely to reduce storage reserves, but apart from host-testing, no studies have been conducted on the effect of stem- or root-boring species on lantana. Stem- and root-feeding species (Cerambycidae) are currently being released or imported into Australia for host-testing (Julien and Griffiths, 1998).

The low germination rate of lantana (Spies and du Plessis, 1987) and the short time during which fruit are viable (Broughton, 1999b) suggests that flower- and fruit-feeding species are unlikely to regulate lantana populations. However, research examining recruitment is required before further conclusions can be drawn.

Of the factors influencing establishment, low number of individuals released accounted for 13 cases of failure. The likelihood of successful establishment can be overcome by releasing more individuals. If more than 30,000 individuals are released (Beirne, 1985), the likelihood of establishment increases to around 80%, and if 5000–30,000 individuals are released, the likelihood of colonization is 40% (Beirne, 1985). However, it may not be possible to increase releases of species with a long generation time, such as Cerambycidae. For example, *P. spinipennis* has a life cycle of 10–12 months (Harley, 1969).

Parasitism and predation did not prevent establishment of an insect species in any case examined in this paper, though the likelihood of control was reduced. External-feeding Lepidoptera are the most susceptible taxa and should not be considered for further releases.

Cultivar preferences were implicated in seven cases of problems with control. Experiments are required to test cultivar preferences because failure of an agent to control lantana can be blamed on preference, rather than examining the reasons for this failure (Neser and Cilliers, 1989). If cultivar preferences do exist, then agents can be targeted against specific cultivars. Neser and Cilliers (1989) suggest that specific cultivars could be exposed to potential biocontrol agents in the country of origin.

REFERENCES

Aldrich, J. M. 1923. Descriptions of lantana gall-fly and lantana seed-fly (Diptera). *Proc. Hawaii. Entomol. Soc.* **5,** 261–263.

Anon. 1993. Successful biocontrol of lantana. *SPC Agric. News* **2,** 1.

Baars, J. R. 1997. Biology and host range of *Teleonemia harleyi* Froeschner (Hemiptera: Tingidae), a potential biological control agent on *Lantana camara* L. (Verbenaceae). *In* "Insects in African Economy and Environment" (H. G. Robertson, Ed.), pp. 131–132. Proceedings of the Entomological Society of Southern Africa (11th Congress) and the African Association of Insect Scientists (12th Congress), Entomological Society of Southern Africa, Stellenbosch.

Barreto, R. W., Evans, H. C., and Ellison, C. A. 1995. The mycobiota of the weed *Lantana camara* in Brazil, with particular reference to biological control. *Mycol. Res.* **1,** 769–782.

Beirne, B. P. 1985. Avoidable obstacles to colonization in classical biological control of insects. *Can. J. Zool.* **63,** 743–747.

Broughton, S. 1999a. "Evaluation of Some Insect Species Introduced for the Biological Control of *Lantana camara* L. in South-East Queensland, Australia," PhD dissertation, The Univ. of Queensland, Brisbane, Australia.

Broughton, S. 1999b. Impact of the seed-fly, *Ophiomyia lantanae* (Froggatt) (Diptera: Agromyzidae), on the viability of lantana fruit in south-east Queensland, Australia. *Biol. Contr.* **15,** 168–172.

Cilliers, C. J. 1982. "An Evaluation of the Effects of Imported Insects on the Weed *Lantana camara* L. in South Africa," Ph.D. dissertation, Rhodes Univ., Grahamstown, South Africa.

Cilliers, C. J. 1983. The weed, *Lantana camara* and the insect natural enemies imported for its biological control into South Africa. *J. Entomol. Soc. Sthn. Afr.* **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. *J. Entomol. Soc. Sthn. Afr.* **50,** 1–13.

Cilliers, C. J. 1987b. The evaluation of three insect natural enemies for the biological control of the weed *Lantana camara*. *J. Entomol. Soc. Sthn. Afr.* **50,** 15–34.

Cilliers, C. J., and Neser, S. 1991. Biological control of *Lantana camara* (Verbenaceae) in South Africa. *Agric. Ecosyst. Environ.* **37,** 57–75.

Common, I. F. B. 1957. The occurrence of *Epinotia lantana* (Busck) (Lepidoptera: Olethreutidae) in Australia. *Proc. Linn. Soc. NSW* **82,** 230–232.

Crawley, M. J. 1986. The population biology of invaders. *Phil. Trans. R. Soc. Lond. B.* **314,** 711–31.

Crawley, M. J. 1989a. Plant life-history and the success of weed biological control projects. *In* "Proceedings of the VII International Symposium on Biological Control of Weeds," pp. 17–26.

Crawley, M. J. 1989b. The successes and failures of weed biocontrol using insects. *Biocontr. News Inform.* **10,** 213–223.

Crutwell-McFadyen, R. E. 1998. Biological control of weeds. *Annu. Rev. Entomol.* **43,** 369–393.

Cullen, J. M., and Snowball, G. J. 1979. Factors limiting the success of biological control organisms. *In* "Australian Entomological Research Conference," pp. 214–222. Lawes, Queensland, Australia.

Davies, J. C., and Greathead, D. J. 1967. Occurrence of *Teleonemia scrupulosa* on *Sesamum indicum* Linn. in Uganda. *Nature* **213,** 102–103.

Davis, C. J., and Krauss, N. L. H. 1962a. Recent developments in the biological control of weed pests in Hawaii. *Proc. Hawaii Entomol. Soc.* **18,** 65–67.

Davis, C. J., and Krauss, N. L. H. 1962b. Recent introductions for biological control in Hawaii-VII. *Proc. Hawaii. Entomol. Soc.* **18,** 125–129.

Davis, C. J., Yoshioka, E., and Kageler, D. 1992. Biological Control of Lantana, Prickly Pear, and *Hämäkua Pämakani* in Hawaii. *In* "Alien Plant Invasions in Native Ecosystems of Hawaii—Management and Research" (P. Stone, C. W. Smith, and J. T. Tunison, Eds), pp. 411–431. Univ. of Hawaii Press, Manoa, Honolulu.

Denton, G., Muniappan, R., and Marutani, M. 1991a. The distribution and biological control of *Lantana camara* in Micronesia. *Micronesica* **3,** 71–81.

Denton, G., Muniappan, R., and Marutani, M. 1991b. Status and natural enemies of the weed, *Lantana camara,* in Micronesia. *Trop. Pest Manage.* **37,** 338–344.

Diatloff, G. 1977. Control biologico de la mala hierba *Lantana camara* por *Octotoma championi* Y *Uroplata* sp. *Agron. Costarricense* **1,** 165–167.

Forno, I. W., and Harley, K. L. S. 1977. The evaluation of biocontrol agents with particular reference to two hispine beetles established on *Lantana camara* in Australia. *In* "Proceedings of the 4th International Symposium on the Biological Control of Weeds," pp. 152–154. Gainesville, FL.

Froeschner, R. C. 1970. *Teleonemia harleyi,* a new species of lantana-feeding lace bug from Trinidad. *Proc. Entomol. Soc. Wash.* **72,** 470–472.

Fullaway, D. T. 1956. Biological control of *Opuntia megacantha* and *Lantana camara* in Hawaii. *In* "Proceedings of the 10th International Congress of Entomology," pp. 549–552. Ottawa, Montreal.

Fyfe, R. V. 1937. The lantana bug, *Teleonemia lantanae* Distant. *J. Counc. Sci. Ind. Res.* **10,** 181–186.

Giesbert, E. F., and Penrose, R. L. 1984. Two new purpuricenine longhorns (Coleoptera: Cerambycidae) from the Tamaulipan biotic province. *Coleopt. Bull.* **38,** 59–65.

Goeden, R. D. 1983. Critique and revision of Harris' scoring system for selection of insect agents in biological control of weeds. *Prot. Ecol.* **5,** 287–301.

Goeden, R. D., and Louda, S. M. 1976. Biotic interference with insects imported for weed control. *Annu. Rev. Entomol.* **21,** 325–342.

Graaff, J. L. 1987. The seedfly *Ophiomyia lantanae* and other factors responsible for reducing germination in *Lantana camara* forms found in Natal. *S. Afr. J. Bot.* **53,** 104–107.

Greathead, D. J. 1968. Biological control of *Lantana:* A review and discussion of recent developments in East Africa. *PANS* **14,** 167–175.

Greathead, D. J. 1971a. A review of biological control in the Ethiopian region. *Commonwealth Inst. Biol. Contr. Tech. Commun.* **5,** 23–25.

Greathead, D. J. 1971b. Progress in the biological control of *Lantana camara* in East Africa and discussion of problems raised by the unexpected reaction of some of the more promising insects to *Sesasum indicum*. *In* "Proceedings of the 2nd International Symposium of the Biological Control of Weeds," pp. 89–94. Rome, Italy.

Gutierrez, J., and Forno, I. W. 1989. Introduction into New Caledonia from Australia of two Hispine phytophages of lantana, *Octotoma scabripennis* and *Uroplata girardi* (Coleoptera: Chrysomelidae). *Acta Oecologica Oecologia Appl.* **10,** 19–30.

Harley, K. L. S. 1969a. Assessment of the suitability of *Plagiohammis spinipennis* (Thoms.) (Col. Cerambycidae) as an agent for the control of weeds of the genus *Lantana* Verbenaceae). 1. Life history and capacity to damage *L. camara* in Hawaii. *Bull. Entomol. Res.* **58,** 567–574.

Harley, K. L. S. 1969b. The suitability of *Octotoma scabripennis* Guer. and *Uroplata girardi* Pic (Coleoptera: Chrysomelidae) for the biological control of *Lantana* (Verbenaceae) in Australia. *Bull. Entomol. Res.* **58,** 835–843.

Harley, K. L. S. 1971. Biological control of *Lantana*. *PANS* **17,** 433–437.

Harley, K. L. S. 1973. Biological control of central and south American weeds in Australia. *In* "Proceedings of the 2nd International Symposium of the Biological Control of Weeds," pp. 4–10. Rome, Italy.

Harley, K. L. S. 1974. Biological control of lantana in Australia. *In* "Proceedings of the 3rd International Symposium of the Biological Control of Weeds," pp. 23–29. Montpellier, France.

Harley, K. L. S., and Forno, I. W. 1992. "Biological Control of Weeds: A Handbook for Practioners and Students," Inkata Press, Melbourne.

Harley, K. L. S., and Kassulke, R. C. 1971. Tingidae for biological control of *Lantana camara* (Verbenaceae). *Entomophaga* **16,** 389–410.

Harley, K. L. S., and Kassulke, R. C. 1974. The suitability of *Phytobia lantanae* (Frick) for biological control of *Lantana camara* in Australia. *J. Aust. Entomol. Soc.* **13,** 229–233.

Harley, K. L. S., Kerr, J. D., and Kassulke, R. C. 1979. Effects in SE Queensland during 1967–72 of insects introduced to control *Lantana camara*. *Entomophaga* **24,** 65–72.

Harley, K. L. S., and Kunimoto, R. K. 1969. Assessment of the suitability of *Plagiohammis spinipennis* (Thoms.) (Col., Cerambycidae) as an agent for control of weeds of the genus *Lantana* (Verbenaceae). II. Host specificity. *Bull. Entomol. Res.* **58,** 787–792.

Harley, K. L. S., and Willson, B. W. 1968. Propagation of a cerambycid borer on a meridic diet. *Can. J. Zool.* **46,** 1265–1266.

Harris, P. 1973a. The selection of effective agents for the biological control of weeds. *Can. Entomol.* **105,** 1495–1503.

Harris, P. 1973b. The selection of effective agents for the biological control of weeds. *In* "Proceedings of the 3rd International Symposium of the Biological Control of Weeds," pp. 75–85. Montpellier, France.

Harris, P. 1991. Classical biocontrol of weeds: Its definition, selection of effective agents, and administrative–political problems. *Can. Entomol.* **123,** 827–849.

Hokkanen, H., and Pimental, D. 1984. New approach for selecting biological control agents. *Can. Entomol.* **116,** 1109–1171.

Holloway, J. K. 1964. Projects in biological control of weeds. *In* "Biological Control of Insect Pests and Weeds" (P. DeBach, Ed.), pp. 650–652. Chapman & Hall, London.

Howard, R. A. 1969. A check list of cultivar names used in the genus *Lantana*. *Arnoldia* **29,** 73–109.

Jayanth, K. P., and Visalaksh, P. N. G. 1992. Suppression of lantana bug *Teleonemia scrupulosa* by *Erythmelus teleonemiae. FAO Plant Prot. Bull.* **40,** 164.

Julien, M. H. 1982. "Biological Control of Weeds: A Catalogue of

Agents and Their Target Weeds," 1st ed., Commonwealth Agricultural Bureau International, Wallingford, UK.

Julien, M. H., and Griffiths, M. W. 1998. "Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds," 4th ed., Commonwealth Agricultural Bureau International, Wallingford, UK.

Kamath, M. K. 1979. A review of the biological control of insect pests and noxious weeds in Fiji (1969–1978). *Fijian Agric. J.* **41,** 55–72.

Krauss, N. L. H. 1953. Notes on insects associated with lantana in Cuba. *Proc. Hawaii. Entomol. Soc.* **15,** 123–125.

Krauss, N. L. H. 1962. Biological control investigations on *Lantana*. *Proc. Hawaii. Entomol. Soc.* **18,** 134–136.

Krauss, N. L. H. 1964. Some leaf-mining chrysomelids of *Lantana* (Coleoptera). *Coleopt. Bull.* **18,** 92–94.

Liddy, J. 1982. Predation of the lantana leafmining beetle by the silvereye in south-eastern Queensland. *Corella* **6,** 123.

Liddy, J. 1985. A note on the associations of birds and lantana near Beerburrum, south-eastern Queensland. *Corella* **9,** 125–126.

Livingstone, D., Jayanthi Bai, S., and Yacoob, M. H. S. 1981. Population dynamics of the lantana bug, *Teleonemia scrupulosa* Stål (Tingidae). *Uttar Pradesh J. Zool.* **1,** 87–90.

Manian, S., and Udaiyan, K. 1992. Altitudinal distribution of the Lantana lace bug *Teleonemia scrupulosa* Stål. in the Anaimalai hills (Western Ghats), India. *Trop. Pest Manage.* **38,** 93–95.

Marohasy, J. 1994. The pest status of *Phenacoccus parvus* Morrison (Homoptera: Pseudococcidae). *Int. J. Pest Manage.* **40,** 337–340.

Marohasy, J. 1997. Acceptability and suitability of seven plant species for the mealybug *Phenacoccus parvus* Morrison (Homoptera: Pseudococcidae). *Entomol. Exp. Appl.* **83,** 239–246.

Marohasy, J. 1998. "Assessing Host Specificity in Weed Biological Control, with Particular Reference to the Lantana Mealybug," PhD dissertation, Entomology Department, Univ. of Queensland, Brisbane, Australia.

Melksham, J. A. 1984. Colonial oviposition and maternal care in two strains of *Leptobyrsa decora* Drake (Hemiptera: Tingidae). *J. Aust. Entomol. Soc.* **23,** 205–210.

Moldenke, H. N. 1973. Flora of Panama. Family 168. Verbenaceae. *Ann. MO Bot. Gdn.* **60,** 41–148.

Muniappan, R., Denton, G. R. W., Brown, J. W., Lali, T. S., Prassad, U., and Singh, P. 1996. Effectiveness of natural enemies of *Lantana camara* on Guam: A site and seasonal evaluation. *Entomophaga* **41,** 167–182.

Muniappan, R., and Viraktamath, C. A. 1986. Status of biological control of the weed, *Lantana camara* in India. *Trop. Pest Manage.* **32,** 40–42.

Neser, S. 1994. Biocontrol of lantana revived. *Plant Prot. News* **35,** 3.

Neser, S., and Cilliers, C. J. 1989. Work towards the biological control of *Lantana camara* perspectives. *In* "Proceedings of the 7th International Symposium on Biological Control of Weeds," pp. 363–369. Rome, Italy.

O'Connor, B. A. 1960. A decade of biological control work in Fiji. *Fijian Agric. J.* **30,** 44–54.

Palmer, W. A., and Pullen, K. R. 1995. The phytophagous arthropods associated with *Lantana camara, L. hirsuta, L. urticifolia,* and *L. urticoides* (Verbenaceae) in North America. *Biol. Contr.* **5,** 54–72.

Palmer, W. A., and Pullen, K. R. 1998. The host range of *Falconia intermedia* (Distant) (Hemiptera: Miridae): a potential biological control agent for *Lantana camara* L. (Verbenaccae). *Proc. Entomol. Soc. Wash.* **100,** 633–635.

Palmer, W. A., Willson, B. W., and Pullen, K. R. 1996. The host range of *Aconophora compressa* Walker (Homoptera: Membracidae): A potential biological control agent for *Lantana camara* L. (Verbenaceae). *Proc. Entomol. Soc. Wash.* **98,** 617–624.

Pemberton, C. E. 1964. History of entomology in Hawaii 1778–1963. *Pacific Insects* **6,** 690–729.

Perkins, B. D. 1966. "Status and Relative Importance of Insects Introduced to Combat Lantana," PhD dissertation, Univ. of Hawaii at Manoa, Honolulu.

Perkins, R. C. L., and Swezey, O. H. 1924. The introduction into Hawaii of insects that attack Lantana. *Hawaiian Sugar Planters' Assoc. Ser. Bull.* **16,** 1–83.

Pimental, D., Glenister, C., Fast, S., and Gallahan, D. 1984. Environmental risks of biological pest controls. *Oikos* **42,** 283–290.

Radunz, L. A. J. 1971. "Some Aspects of the Preferential Behaviour of *Teleonemia scrupulosa* Stål, Towards Its Host Plant *Lantana camara,*" Undergraduate honors thesis, Entomology Department, The Univ. of Queensland, Brisbane, Australia.

Rao, R. 1920. Lantana insects in India: Being the report on an inquiry into the efficiency of indigenous insect pests as a check against the spread of Lantana in India. *Mem. Indian Dept. Agric. Entomol. Serv.,* **5.**

Rao, V. P., Ghani, M. A., Sankaran, T., and Mathur, K. C. 1971. A review of the biological control of insects and other pests in South-East Asia and the Pacific Region. *Commonwealth Ins. Biol. Contr. Tech. Commun.* **6.**

Riley, E. G., and Balsbaugh, E. U. 1988. Two middle American leaf beetles (Coleoptera: Chrysomelidae) newly recorded from the United States. *Entomol. News* **99,** 148–152.

Scheibelreiter, G. K. 1980. Biological control of *Lantana camara* L. (Verbenaceae) in Ghana. *Z. Angew. Entomol.* **90,** 99–93.

Scott, L. J., Graham, G. C., Hannan-Jones, M., and Yeates, D. K. 1997. DNA profiling resolves the limited importance of flower color in defining varieties of *Lantana camara*. *Electrophoresis* **18,** 1560–1563.

Simmonds, H. W. 1929. The life history of *Teleonemia lantanae* Distant. *Fiji Agric. J.* **2,** 36–39.

Smith, L. S., and Smith, D. A. 1982. "The Naturalised Lantana Camara Complex in Eastern Australia," Queensland Botany Bulletin No. 1, Queensland Department of Primary Industries, Brisbane, Australia.

Spencer, K. A. 1990. "Host Specialization in the World Agromyzidae (Diptera)," Kluwer Academic, Dordrecht, Germany.

Spies, J. J. 1984. Embryo sac development of some South African cultivars of *Lantana camara*. *Bothalia* **15,** 161–166.

Spies, J. J., and du Plessis, H. 1987. Sterile *Lantana camara:* Fact or theory. *South African J. Plant Soil* **4,** 171–174.

Stirton, C. H. 1977. Some thoughts on the polyploid complex *Lantana camara* L. (Verbenaceae). *In* "Proceedings of the Second National Weeds Conference," pp. 321–340. Balkema, Cape Town.

Swarbrick, J. T. 1985. History of the lantanas in Australia and origins of the weedy biotypes. *Plant Prot. Q.* **1,** 115–121.

Swarbrick, J. T., and Donaldson, J. F. 1991. Host range studies with the lantana mealybug (*Phenacoccus parvus* Morrison). *Plant Prot. Q.* **6,** 68–69.

Swarbrick, J. T., Willson, B. W., and Hannan-Jones, M. A. 1995. The biology of Australian Weeds 25. *Lantana camara* L. *Plant Prot. Q.* **10,** 82–95.

Taylor, E. E. 1989. A history of biological control of *Lantana camara* in New South Wales. *Plant Prot. Q.* **4,** 61–65.

Thakur, M. L., Ahmad, M., and Thakur, R. K. 1992. Lantana weed (*Lantana camara* var. *aculeata* Linn.) and its possible management through natural insect pests in India. *Indian Forester* **118,** 466–488.

Wapshere, A. J. 1985. Effectiveness of biological control agents for weeds: Present quandaries. *Agric. Ecosyst. Environ.* **13,** 261–80.

Waterhouse, D. F., and Norris, K. R. 1987. "Biological Control—Pacific Prospects," Inkata Press, Melbourne, Australia.

Willson, B. W. 1974. Diet-rearing the lantana insect *Plagiohammis spinipennis* (Thoms.) (Col. Cerambycidae). *Qld. J. Agric. Animal Sci.* **41,** 405–412.

Willson, B. W. 1993. A renewed attempt at the biological control of *Lantana camara*. *In* "Proceedings of the 10th Australian Weeds Conference and 14th Asian Pacific Weed Science Society Conference," pp. 107–110. Weed Society of Queensland, Brisbane, Australia.

Winder, J. A. 1980. "Factors Affecting the Growth of *Lantana* in Brazil," PhD dissertation, Univ. of Reading, England.

Winder, J. A., and Harley, K. L. S. 1982. The effects of natural enemies on the growth of *Lantana* in Brazil. *Bull. Entomol. Res.* **72,** 599–616.

Winder, J. A., and Harley, K. L. S. 1983. The phytophagous insects on *Lantana* in Brazil and their potential for biological control in Australia. *Trop. Pest Manage.* **29,** 346–362.

Winder, J. A., Harley, K. L. S., and Kassulke, R. C. 1984. *Uroplata lantanae* Buzzi & Winder (Coleoptera: Chrysomelidae: Hispinae), a potential biological control agent of *Lantana camara* in Australia. *Bull. Entomol. Res.* **74,** 327–340.

Winder, J. A., Sands, D. P. A., and Kassulke, R. C. 1988. The life history, host specificity and potential of *Alagoasa parana* Samuelson (Coleoptera: Chrysomelidae) for biological control of *Lantana camara* in Australia. *Bull. Entomol. Res.* **78,** 511–518.

Winder, J. A., and van Emden, H. F. 1980. Selection of effective biological control agents from artificial defoliation/insect cage experiments. *In* "Proceedings of the 5th International Symposium on the Biological Control of Weeds," pp. 415–439. Brisbane, Australia.