

The invasive '*Lantana camara* L.' hybrid complex (Verbenaceae): a review of research into its identity and biological control in South Africa

A.J. Urban*, D.O. Simelane*, E. Retief, F. Heystek, H.E. Williams & L.G. Madire

Agricultural Research Council-Plant Protection Research Institute, Private Bag X134, Queenswood, 0121 South Africa

Recent progress in the nomenclature and genetics of the hybrid-complex 'lantana' is summarized as it pertains to sourcing the best-adapted natural enemies for its biological control. Reasons are given for viewing the whole array of invasive taxa within *Lantana* L. sect. *Camara* Cham. (Verbenaceae) as a syngameon, and for surveying natural enemies of *camara*-like *Lantana* entities between Florida and Uruguay. To improve the degree of biological control of lantana, additional agents have been selected, evaluated and found suitable for release in South Africa. The quarantine evaluation and current status of 30 candidate biological control agents obtained from the New World is summarized. Of these, seven were found to be suitable for release, according to given criteria, and two new agents, *Aceria lantanae* (Cook) (Acari: Eriophyidae) and *Ophiomyia camarae* Spencer (Diptera: Agromyzidae), are improving control of lantana in humid, frost-free areas. No significant non-target effects have been detected. Information on the distribution and abundance of 17 agents and lantana-associated insects established in South Africa is presented: several are mainly coastal and they are scarce overall. Agent proliferation is constrained by a combination of climatic incompatibility, acquired natural enemies and, probably, the broad spectrum of allelochemicals present in the allopolyploid hybrids within the *L. camara* complex. In the case of lantana, biological control plays a subsidiary role in support of essential mechanical-plus-chemical control. Cost benefits justify the continued development of additional agents.

Key words: *Lantana* nomenclature, genetics, exploration, agent development, *Aceria lantanae*, *Coelocephalopion camarae*, *Falconia intermedia*, *Longitarsus bethae*, *Ophiomyia camarae*, *Orthonama* (= *Leptostales*) *ignifera*, *Passalora* (= *Mycovellosiella*) *lantanae*, allelochemicals, allopolyploidy.

INTRODUCTION

A scourge of the Old World, 'lantana' (Fig. 1), widely, but contentiously, known as '*Lantana camara* L.' (Verbenaceae), is one of the most ecologically and economically harmful invasive alien plants of the tropical, subtropical and warm temperate regions of Africa, southern Asia, Australia and Oceania (Day *et al.* 2003a). It is considered to be a man-made weed, comprising an array of hundreds of named horticultural selections and hybrids bred mainly in Europe from unrecorded parental species obtained from the New World after 1492 (Stirton 1977). These garden ornamentals, prized for their multicoloured flowers, ease of propagation and hardiness, were distributed worldwide, often between lantana clubs, especially in the 1800s. With the help of frugivorous birds, the shrubs invade natural ecosystems, where they transform the indigenous vegetation into impenetrable thickets of lantana,

which diminish natural pasturage, reduce productivity of stock-farming, poison cattle, obstruct access to water sources and plantations, reduce biodiversity and devalue the land (Day *et al.* 2003a).

Records indicate that lantana was introduced into South Africa in 1858 at Cape Town, Western Cape Province (WC), where it spread very little under Mediterranean climatic conditions, and in 1883 at Durban, KwaZulu-Natal Province (KZN) (Stirton 1977), where it flourished under subtropical conditions (Fig. 2). It was declared a noxious weed in 1946 in KZN, which contained 80 % of the South African infestation, doubling in area approximately every decade (Marr 1964; Wells & Stirton 1988). Gauged by recent requests from the public for advice on lantana control, the weed is currently increasing in density and spreading mainly in the provinces of Mpumalanga (MP) and Limpopo (LP), as well as in the North West (NW), Eastern Cape (EC), Gauteng (GP) and the southern part of

*To whom correspondence should be addressed.
E-mail: urbana@arc.agric.za / simelaned@arc.agric.za

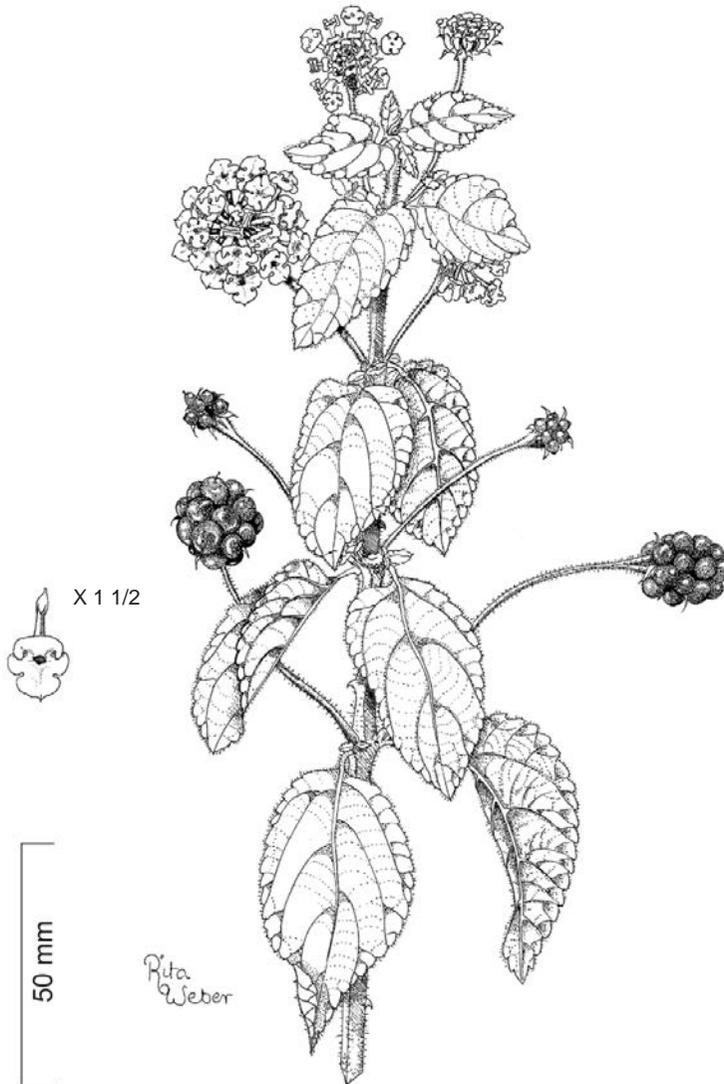


Fig. 1. *Lantana camara* L. (*sensu lato*) (Drawn by R. Weber, first published in Stirton (1978), South African National Biodiversity Institute, Pretoria).

WC, *i.e.* mainly in the hotter and outer parts of its current distribution (Fig. 2). By 1998, lantana was estimated by experts to have infested over 2.2 million ha in South Africa, which, if condensed, would completely cover an area of more than 69 000 ha (Versfeld *et al.* 1998). A recent, statistically valid, national, invasive alien plant survey found that lantana now covers 560 000 ha of the landscape, including riparian areas (Kotze *et al.* 2010).

Biological control is seen as the ideal solution – environmentally friendly and self-sustaining.

Research, in various countries, into the biological control of lantana has been undertaken for more than a century, and has produced a plethora of publications (Muniappan *et al.* 1992) and the involvement of 41 biological control agents (Day *et al.* 2003a). However, even with the establishment of up to 17 agents per country, the suppression of lantana in most of the Old World, excluding some islands in the Pacific (Muniappan *et al.* 1996), is still inadequate (Day *et al.* 2003a). In an attempt to improve biological control of

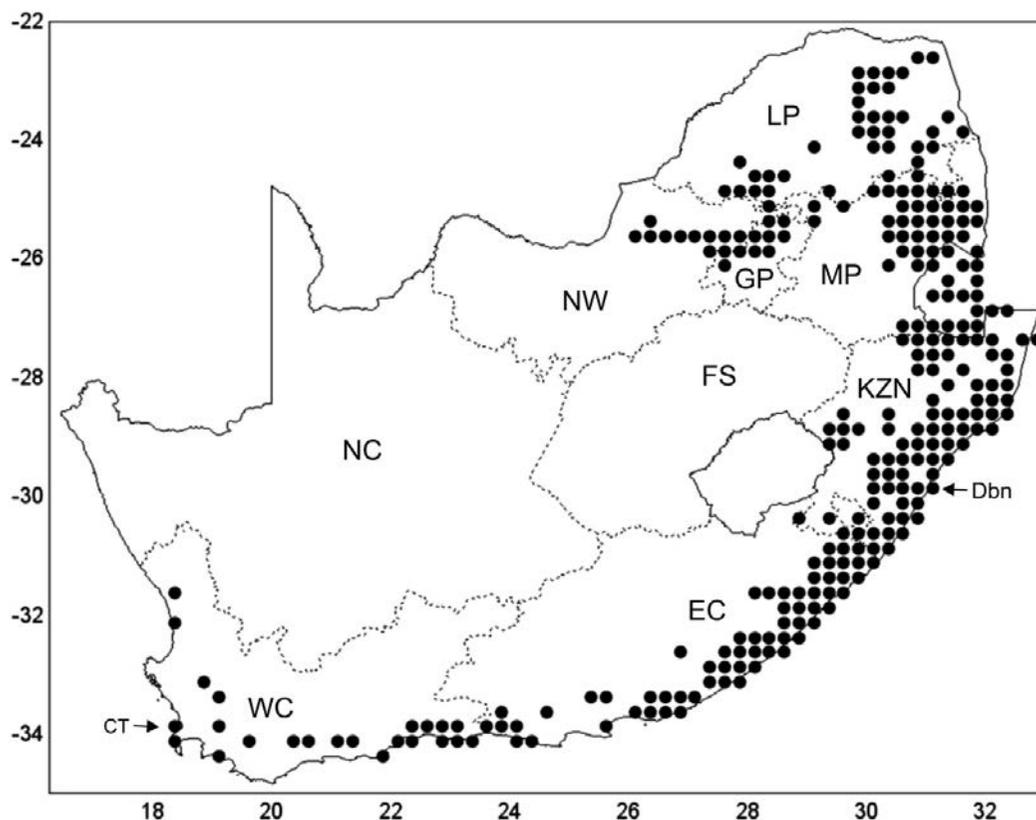


Fig. 2. Distribution of *Lantana camara* L. (*sensu lato*) in South Africa. (Drawn by L. Henderson. Data source: SAPIA database, Agricultural Research Council-Plant Protection Research Institute, Pretoria). Provinces: WC, Western Cape; EC, Eastern Cape; NC, Northern Cape; FS, Free State; KZN, KwaZulu-Natal; NW, North West; GP, Gauteng; MP, Mpumalanga; LP, Limpopo. Cities: CT, Cape Town; Dbn, Durban.

lantana, the work reported here focuses on the primary development (*i.e.* selection, evaluation and release) of additional agents for use in South Africa.

Previous review articles have covered various aspects of lantana and its biological control (Neser & Cilliers 1990; Cilliers & Neser 1991; Swarbrick *et al.* 1998; Baars & Neser 1999; Broughton 2000; Day *et al.* 2003a,b; Sharma *et al.* 2005; Day & Zalucki 2009), with the illustrated monograph of Day *et al.* (2003a) as the most comprehensive source of global information for lantana biological control practitioners. The present review provides: (i) a summary of recent advances in the nomenclature and genetic composition of lantana as it pertains to exploration for the best-adapted natural enemies; (ii) details, for completeness, of the primary lantana biological control agent development work performed in South Africa during slightly

more than the decade since the previous review (Baars & Neser 1999); (iii) brief accounts of agent establishment, abundance and impact in South Africa; (iv) a discussion of constraints on agent proliferation; and (v) a summary of the implications for control of the weed and for further research.

NOMENCLATURE, GENETICS AND EXPLORATION

Nomenclature

Lantana is in the throes of an identity crisis. Linnaeus (1753) described briefly, in Latin, prickly, red- or yellow-flowered *Lantana Camara* [sic], and prickly, red-flowered *L. aculeata* L. from an array of garden and horticulturally-selected plants taken from gardens in Europe (although he stated their habitat to be tropical America). As syntypes, he listed three previously published descriptions

for the former and four for the latter, and deposited an array of voucher herbarium specimens without designating any particular one as the holotype. In 1934, the leading taxonomist on *Lantana* synonymized the latter entity as *L. camara* var. *aculeata* (L.) Moldenke, and that found taxonomic acceptance. In 1983, Moldenke & Moldenke designated one of Linnaeus' herbarium specimens, namely LINN 783.4, as the lectotype of *L. camara* L. (Sanders 2006). When R.W. Sanders of the Botanical Research Institute (BRI), Texas, U.S.A., examined the previously unseen underside of the leaf of this lectotype, he found the trichomes on the veins and interveinal tissue to be pilose, which, along with other characters, indicated that this is a specimen of a valid, wild species, taxonomically distinct from weedy lantana (Sanders 2006). Linnaeus (1753) stated that *Lantana Camara* 'Habitat in America calidiorē', i.e. lives in 'hot' (tropical) America; Moldenke thought that this type specimen was probably collected from a garden in Sweden, although the 'type locality' has been given as Brazil (Munir 1996); Sanders (2006) states that this species is indigenous to the Greater Antilles, Mexico and northwestern South America. As this type specimen is taxonomically distinct from weedy lantana, the conventional practice, throughout the voluminous, scientific literature, of applying the name '*Lantana camara* Linnaeus' to weedy lantana is taxonomically incorrect (Sanders 2006).

The numerous horticultural lantana taxa that became invasive plants in the Old World differ from wild *L. camara* L. in the New World, morphologically, karyologically, physiologically and ecologically, as evidenced, for example, by their greater (up to hexaploid) chromosome complement (Stirton 1977; Spies 1984a), greater concentration and broader spectrum of allelochemicals (Hart *et al.* 1976), greater growth vigour, reproductive vigour and resistance to natural enemies (Swarbrick *et al.* 1998; Day *et al.* 2003a; Sharma *et al.* 2005; Day & Zalucki 2009), and greater invasiveness (Maschinski *et al.* 2010). Weedy lantana therefore merits a different group name (Sanders 2006).

Morphologically different taxa of weedy lantana interbreed freely, producing hybrids of intermediate form, which makes it extremely difficult to apply formal taxonomic nomenclature to such a complex group (Spies 1984a; Munir 1996). Consequently, scientists refer to the whole array of weedy lantana taxa by a variety of informal names, such

as: the '*L. camara* complex' (Stirton 1977; Spies 1984a; Munir 1996; Sanders 2006) comprising many 'cultigens' (Stirton 1999; Sanders 2006) or 'invasions' (Stirton 1999); '*L. camara* hybrid complex' (Stirton 1977; Naser & Cilliers 1990; Baars 2000a; de Kok 2002; Maschinski *et al.* 2010); '*L. camara*' i.e. the '*L. camara* complex of species, hybrids, varieties, forms or whatever status is afforded to the entities [that comprise] a very plastic continuum in which hybridization is still occurring continuously' (Naser & Cilliers 1990); '*L. camara* species aggregate' (Johnson 2007, 2011; GRIN 2011); '*L. camara* aggregate species' (Spies & Stirton 1982b; Stirton 1999; de Kok 2002; Johnson 2007, 2011); and '*L. camara* hort.' (GRIN 2007; Randall 2007; Henderson 2009; Urban 2010; Urban *et al.* 2010a,b, 2011). Many of these informal names are not completely suitable for weedy lantana, for the following reasons. The name '*L. camara* complex' is ambiguous because it is also used to refer to a group of valid species within *Lantana* sect. *Camara* (Day *et al.* 2003a; Day & Zalucki 2009) or the invasive entities within or the whole of *Lantana* sect. *Camara* (Sanders 2006). 'Hybrid complex', 'species aggregate' (Heywood 1964) and 'aggregate species' (singular) all, strictly speaking, do not include both the hybrids and the valid species that have also been introduced and become naturalized and weedy, and 'hort.' is conventionally applied to only a single sport, hybrid or cultivar (IPNI 2004) rather than a whole array of entities.

The scientific name '*L. camara* L.' has been widely misapplied to many or all species and hybrids within *Lantana* sect. *Camara* (Sanders 2006) and a different appellation is required for the weedy complex. By careful examination of the morphology and distribution of leaf trichomes of herbarium specimens that specialists had called '*Lantana camara* L.' over the last two-and-a-half centuries, Sanders (2006) ascertained that pilose-morph and setose-morph specimens had become permanently scarce (<14 % and <7 %, respectively) by 1831, and that strigose-morph and mixed-(mainly strigose plus pilose) morph specimens had become common (about 51 % and 49 % respectively) since then. He attributed this shift in the morphology of '*L. camara* L.' over time to 'Horticultural selection [that] developed aggressively growing allopolyploid cultigen species and subspecies that became naturalized, often as pernicious weeds' (Sanders 2006). He found 'SCD' entities, i.e. with strigose-haired, cordate, dull

leaves to be currently dominant in the horticultural trade, and globally widespread, and named an SCD 'cultigen species of hybrid origin' *Lantana strigocamara* R.W. Sanders (Sanders 2006). *Lantana* × *strigocamara* is also accepted as legitimate (MOBOT 2010; RBGK 2010). He has not yet named the various other hybrid entities within weedy lantana. This new name, *L. (×)strigocamara*, has not been used much as yet – exceptions such as Maschinski *et al.* (2010) being rare. Publications since 2006 show that almost all researchers have continued to use the entrenched name '*L. camara* L.' when referring to any or all varieties of weedy lantana, despite its taxonomic inappropriateness.

It is highly desirable, but extremely difficult (Munir 1996) or impossible (Spies 1984a), to give a definitive name to each lantana variety that one is working on. For simplicity, each variety is usually named according to place of occurrence plus the colour of the aging flowers (Scott *et al.* 1997; Day *et al.* 2003a). However, the reliability of such names is questionable, because lantana varieties interbreed freely in the field, producing hybrids of intermediate form (Spies 1984a). An attempt was made to improve reliability by utilizing many (about 70) morphological characters (Stirton & Erasmus 1990). This was simplified as a formula, listing the state of 11 fairly stable, macroscopic, vegetative and reproductive characters, which was used to identify and name 17 of the core 'variants' of lantana in KZN (Stirton 1999) and could possibly be used more widely as a practicable method of naming lantana varieties.

The name '*L. camara* L. (*sensu lato*)' that is widely used for weedy lantana (Stirton 1977; Spies 1984a; Naser & Cilliers 1990; Munir 1996; Baars & Naser 1999; de Kok 2002; Day *et al.* 2003a; Day & Zalucki 2009) is correct under both the International Code of Botanical Nomenclature and the International Code of Nomenclature for Cultivated Plants (H.F. Glen, pers. comm.) and is used here, abbreviated to '*L. camara* (*s.l.*)'. In accordance with Day *et al.* (2003a), 'We reserve the common name 'lantana' specifically for the weedy taxa of the [genus *Lantana* L.] section *Camara* [Cham.]', and we refer to the component entities as 'varieties'.

Genetic composition

Lantana is a complex of genetically modified plants, produced by selection and hybridization. On morphological grounds, Sanders (2006) deduced the putative parents of the globally wide-

spread, weedy *L. (×)strigocamara* to be *L. camara* L. subsp. *aculeata* (L.) R.W. Sanders from the West Indies and Mexico to northern South America and *L. nivea* Vent. subsp. *mutabilis* (W.J. Hook) R.W. Sanders from southern Brazil to Argentina, with some input from *L. scabrida* Sol. in Aiton from the West Indies and Mexico, and/or, *L. splendens* Medik. from the Bahamas, and possibly *L. hirsuta* M. Martens & Galeotti from Mexico.

South African specimens of weedy lantana that Sanders has examined are mostly hybrids between *L. nivea mutabilis* and *L. camara aculeata* (M.D. Day, pers. comm.). Others appear to have input from either of the above parents plus *L. scabrida*, *L. horrida* Kunth subsp. *tiliifolia* (Cham.) R.W. Sanders ined. from S. Brazil, *L. (×)strigocamara*, *L. hirsuta*, possibly *L. depressa* Small from Florida and the Callowiana Hybrid Group (*L. (×)strigocamara* × *L. depressa* var. *depressa*), and there is also some pure *L. nivea mutabilis* present (M.D. Day, pers. comm.).

Australian weedy lantana comprises a similarly wide array of hybrids, according to Sanders, with the dominant parents being *L. nivea mutabilis* and *L. horrida tiliifolia*, both from southern Brazil, and some pure *L. camara aculeata* and *L. hirsuta hirsuta* being present (M.D. Day, pers. comm.).

Molecular genetic studies have clarified many phylogenetic relationships, and it was hoped that DNA work would do the same for weedy lantana (Day & Hannan-Jones 1999; Day *et al.* 2003a; Day & Urban 2004). Under the leadership of M.D. Day of the Alan Fletcher Research Station (AFRS) in Brisbane, hundreds of specimens of *Lantana* taxa have been collected from many countries in the Old and New Worlds, by collaborators including the staff of the South African Agricultural Research Council-Plant Protection Research Institute (ARC-PPRI), and duplicate samples have been subjected to morphological analysis by R.W. Sanders of BRI in Texas, and DNA analysis by L.J. Scott of the University of Queensland or R. Watts of the Commonwealth Scientific and Industrial Research Organization (CSIRO), Australia, in research that is still under way.

Initial work showed clustering of random amplification of polymorphic DNA (RAPD) markers on a cladogram that indicated more genetic similarity between lantana varieties of different flower colour in the same area, than between varieties of the same flower colour in different areas (Scott *et al.* 1997). This may be the result of the continu-

ous, local hybridization that occurs in the field (Spies 1984a). It indicates the limited importance of flower colour alone in differentiating lantana varieties (Scott *et al.* 1997). Surprisingly, the specimens of wild, orange-flowered *L. urticifolia* L. [sic] from Mexico, which Scott *et al.* (1997) included as a potential outgroup, clustered in the midst of all the specimens of Australian pink and pink-edged red weedy lantana, indicating the extremely close relationship between this wild species and the weedy hybrids (Scott *et al.* 1997; Day *et al.* 2003a; Day & Zalucki 2009).

Subsequent studies using RAPD markers (Scott *et al.* 2002) showed that specimens of Australian weedy lantana are far more closely related to specimens of *L. urticifolia* Mill. from Mexico than to specimens of *L. tileaefolia* [sic] Cham. and *L. glutinosa* Poepp. from S. Brazil (unpublished cladogram of Scott *et al.* (2002) supplied by M.D. Day, pers. comm.). *Lantana urticifolia* was also found to have been the source plant of biological control agents with the highest frequency of establishment (Day & Hannan-Jones 1999; Day *et al.* 2003a; Day & Zalucki 2009). However, these findings were based on the identification of specimens by Sanders, who misapplied the name *L. urticifolia* prior to 2006, to *L. camara* L. and *L. horrida* (Sanders 2006). These DNA results therefore indicate that Australian weedy lantana is closely related to *L. camara* L., which is native to the West Indies, Mexico, Central America and northwestern South America, and possibly to *L. horrida* though very few of the wild *Lantana* species were included in the work by Scott *et al.* (2002).

Recent DNA work by Watts (2010) indicates that plant specimens from the Americas and Australia, which Roger Sanders identified as four valid *Lantana* species and 12 putative hybrids, all within *Lantana* sect. *Camara*, are 'probably derived from a single, widespread [ancestral] species with considerable morphological variation, rather than from a horticultural crossing of a multitude of species'. He interprets this to mean that *Lantana* section *Camara* is a single species. By priority, that species would be *L. camara* L. This single-species interpretation contradicts the taxonomic differentiation of these wild species on morphological grounds, as well as the central dogma, based on horticultural (Howard 1969), morphological (Sanders 2006) and karyological evidence (Spies & Stirton 1982a,b; Spies 1984a,b,c), that weedy lantana comprises mainly interspecific hybrids. However, compari-

son with Watts' (2010) successful differentiation of species within *Lantana* sect. *Calliorheas* [sic], using the same DNA technique, would suggest that the entities within *Lantana* sect. *Camara* may well be closely related species, subspecies and hybrids. A group of closely related plant taxa at about the species level that hybridize with one another has been referred to by a number of informal descriptors (Stuessy 2009). 'Syngameon' appears to describe the lantana complex well, as 'the sum total of species or semispecies [*i.e.* intermediates between species and subspecies] linked by frequent or occasional hybridization in nature; a hybridizing group of species; the most inclusive interbreeding population' (Grant 1957, cited by Stuessy 2009).

Phylogeographic affinities indicated by the most recent DNA results (Watts 2010), combined with Sanders' most recent identifications (M.D. Day, pers. comm.) of the duplicate specimens are, firstly, that most specimens of Australian weedy lantana are most-closely related to each other, and then to a specimen (MD 006A) of weedy lantana from South Africa. Secondly, the clade of Australian and South African specimens is more similar to a group of predominantly eastern specimens, from the West Indies, Venezuela, Brazil and Florida, than to a group of predominantly western ones, from Mexico, Guatemala and Texas. This contradicts the earlier DNA findings by Scott *et al.* (2002), but corroborates the morphology-based interpretation by Sanders (2006) that the provenances of the dominant parents of weedy lantana are the West Indies and southeastern Brazil, with a lesser input from Mexico. Exploration should therefore be refocused eastwards from Central America (Watts 2010).

As this study of morphology and genetics is ongoing, a clearer picture may emerge when more specimens from the whole of the native range of *Lantana* sect. *Camara* have been analysed, and the DNA methods and cladograms have been published.

Exploration for the best-adapted natural enemies

For biological control, the practical value of plant taxonomic studies is to pinpoint the native home of the target weed, to facilitate exploration for the best-adapted, and possibly most effective natural enemies. If the single-species interpretation by Watts (2010) is correct, the native home of the weedy taxa would be the same as that of the wild

taxa in *Lantana* sect. *Camara*, *i.e.* stretching from Texas/Florida to northern Argentina/Uruguay (Day & Zalucki 2009). The centre of diversity of the genus *Lantana* is apparently Central America, northern South America and the West Indies (Day *et al.* 2003a). However, the centre of the native range of *Lantana* sect. *Camara*, is in the vicinity of Colombia/Equador/Peru, which is also in the equatorial region of highest biological diversity. Although this area has been explored to some extent for natural enemies of lantana (Neser & Cilliers 1990), further surveys in this area may be rewarding.

Alternatively, if the dogma is correct that lantana comprises many interspecific hybrids, both natural and artificial, one should explore in the native homes of the parents of the hybrids. If Sanders' (2006) interpretation of the morphology is correct, the dominant parents are mainly from the West Indies and southeastern Brazil, with a lesser input from Mexico. Most of the range of these putative parents has been explored during substantive surveys of natural enemies of *Lantana* spp. in sect. *Camara*, which were undertaken in Mexico (Koebele in Perkins & Swezey 1924; Palmer & Pullen 1995), the West Indies and Central America (Kraus & Mann in Day *et al.* 2003a) and southeastern Brazil (Winder & Harley 1983; Barreto *et al.* 1995). Further exploration for promising phytophages and pathogens on *camara*-like *Lantana* entities in these areas was carried out by the ARC-PPRI, and these candidate agents are considered below.

As the provenances of the putative dominant and lesser parents have already been thoroughly explored, it may be rewarding to now explore the area inbetween, namely from the Guianas to Paraguay. One phytophage from *camara*-like *Lantana* species in this area, namely *Leptobyrsa decora* Drake (Hemiptera: Tingidae) from Peru, established on lantana in Australia (Day *et al.* 2003a), but not in South Africa, despite numerous releases (Julien & Griffiths 1998), and one pathogen, namely *Septoria* sp. (Mycosphaerellales: Mycosphaerellaceae) from Equador, has been found not to be pathogenic to the South African varieties of lantana tested thus far. However, two other candidates, namely *Longitarsus columbicus columbicus* Harold (Coleoptera: Chrysomelidae) from Venezuela and *Puccinia lantanæ* Farl. (Pucciniales: Pucciniaceae) from Peru, look very promising in quarantine, as they are both damag-

ing to several South African varieties of weedy lantana (Baars 2001a; Thomas & Ellison 2000), and the latter candidate is harmless to at least one species in *Lantana* section *Calliorea*s (Renteria B. & Ellison 2004) to which the indigenous African and Indian species belong (Day *et al.* 2003a).

An altogether different approach would be to introduce lantana taxa that are weedy in the Old World, into the New World, and collect the (best-adapted) natural enemies that colonize them (Neser & Cilliers 1990; Cilliers & Neser 1991). Such deliberate introductions would probably be considered unethical today, because of the unacceptably high risk of introducing weeds into new countries. However, horticultural lantana varieties were introduced into the New World nearly two centuries ago (Stirton 1977; Swarbrick *et al.* 1998; Day *et al.* 2003a; Sanders 2006), where they interbreed with (Sanders 1987, 2006) and threaten the survival of wild *Lantana* spp. (Maschinski *et al.* 2010). Exploration in the New World should definitely include surveying the horticultural varieties of *camara*-like *Lantana* growing there, as these may yield the best-adapted natural enemies for use against the horticultural selections of lantana that have become weedy in the Old World.

Exploration work should be planned so as to address the greatest need, which is for natural enemies that are adapted to continental climatic conditions with a dry winter (Cilliers & Neser 1991). In the northwestern quadrant of South America, there may be areas with a suitable climate in the foothills of the Andes, which could be found using climate-matching programmes.

PRINCIPLES OF AGENT DEVELOPMENT IN SOUTH AFRICA

By analogy with the development of plant protection chemicals, we take weed biological control agent 'development' to mean the process of obtaining a promising natural enemy of an invasive alien plant from its native home, evaluating it in quarantine as a candidate biological control agent, and, if adequately host-specific and potentially damaging, releasing it as a biological control agent in the country of introduction. The process includes compliance with governmental regulations, both for natural enemy collection in, movement within and export from the source country, usually in collaboration with the staff of an organization of that country, and for importa-

tion into and release from quarantine in the recipient country. Agent development is essentially the adding of host-specificity damage-potential data to the known biological information on a phytophage or pathogen, indicating its suitability for introduction into the target area. Agent development is the *sine qua non* of biological control.

For lantana, biological control agent development was initiated by research personnel of Hawaii (U.S.A.) in 1902 (Perkins & Swezey 1924), and continued by those of Australia (Harley 1971; Winder & Harley 1983; Palmer & Pullen 1995; Day *et al.* 2003a), the United Kingdom (Greathead 1968; Evans 1987; Thomas & Ellison 2000), and South Africa (Baars & Naser 1999; Morris *et al.* 1999).

The strategy of the current lantana biological control research carried out in South Africa (Naser & Cilliers 1990; Cilliers & Naser 1991; Baars & Naser 1999; Morris *et al.* 1999; Urban *et al.* 2001a; Day & Urban 2004) has been to introduce new agents, to apply increasing stress to lantana in general, and also to target directly the niches on the plant (roots, stems, flowers) that are most under-utilized by the established biological control agents, and to focus on the climatic zone (highveld) that is most sparsely colonized by the established agents. During the earlier phase, 1960–1986, use was made exclusively of agents developed in other countries (Oosthuizen 1964; Cilliers & Naser 1991). Since 1987, South Africa has mainly performed primary agent development, and passed the candidates and new agents on to collaborators in other countries (Baars & Naser 1999).

Taxonomic uncertainties justified the current practical approach of collecting promising natural enemies from undetermined, *camara*-like *Lantana* taxa, *i.e.* species and hybrids that appeared to be within *Lantana* sect. *Camara*. The source plants were usually recorded as *Lantana cf. camara* or *Lantana ?camara*. The collecting trips were very brief, mostly of about two-weeks duration, and usually in autumn. The countries explored included Florida (U.S.A.), Cuba, Jamaica, Dominican Republic, Mexico, Guatemala, Venezuela and Brazil. Each natural enemy was collected from several *Lantana* entities and sites, when possible, in an attempt to provide a genetic stock that could utilize a range of weedy lantana varieties and climatic zones.

To incorporate the variability within the target weed during quarantine evaluation of the candi-

date agents, use was made of a living reference collection of a single mother plant of each of ten of the most common South African varieties of *L. camara* (*s.l.*), which were propagated vegetatively.

Criteria for suitability of a candidate for release into Africa were considered with due caution, because of global concerns about possible non-target impacts of biological control agents (Moran *et al.* 2005). Physiological host range was determined by measuring feeding, oviposition and development on a range of test plants, selected according to the centrifugal, phylogenetic method (Wapshere 1974), under no-choice conditions. Behavioural host range, showing the realistically-probable relative rates of utilization of target and physiologically susceptible non-target plants, was then determined under 'naturalistic' conditions that enabled the adult insects to exercise behavioural preferences (Baars 2000a). Different criteria were used with different candidates. The host-suitability criteria of Maw (1976) or Wan & Harris (1997) were used to assess the risk of at least two candidates. Suitability of most arthropod candidates was assessed according to the criteria proposed by Baars *et al.* (2003), namely: (i) the risk of utilizing non-target plants must be less than 25 % of that of the target weed, when assessed under 'naturalistic' conditions; and (ii) the potential to reduce the rate of growth or reproduction of the target weed must be demonstrated. For risk assessment of insects, oviposition and progeny development to the adult stage were measured on the target plant, and on non-target plants found to be physiologically susceptible in no-choice tests, which were exposed to adults of the candidate agent in a well-replicated, multi-choice Latin square or similar layout in a large (4 × 4 × 2 m), walk-in cage with a through-flow stream of fresh air. Suitability criteria for fungal candidates were: (i) pathogenicity to the target weed; (ii) non-pathogenicity to non-target plants selected according to the centrifugal, phylogenetic method of Wapshere (1974); and (iii) demonstrated potential to reduce the rate of growth or reproduction of the target weed.

Lantana agent development by ARC-PPRI during the last 23 years encompassed the selection and quarantine evaluation of 30 candidate agents, seven of which were found to be suitable for release into Africa, 15 were rejected by the researchers (because of inability to breed sustainably on

weedy South African varieties of lantana, or insufficient host specificity), seven were shelved (where congeners were given priority, or because of uncertain specificity), and one is currently being evaluated (Urban *et al.* 2003) (Table 1).

CANDIDATE AGENTS

The candidate lantana biological control agents dealt with in South Africa during 1987–2010 are listed alphabetically below, with a summary of origin, biology, damage, specificity, impact and features of special interest.

Aceria lantanae (Cook)

(Acari: Trombidiformes: Eriophyidae)

The lantana flower gall mite, *A. lantanae*, feeds primarily on undifferentiated flower buds, which are induced to develop into a large gall comprising a mass of very small green leaves, instead of an inflorescence (Cook 1909). Gallings can markedly reduce seed production and therefore, potentially, the rate of increase in density and spread of the weed (Craemer & Nesar 1990; Nesar 1998). This mite was reportedly first redistributed in an attempt to suppress weedy lantana in Florida, U.S.A. (Keifer & Denmark 1976), and was proposed by Cromroy (1978, 1983) as a candidate for biological control of lantana in the Old World.

Flower galls were collected from orange-flowered *camara*-like *Lantana* entities, and pink-flowered *L. camara* (*s.l.*) in countries in and around the Gulf of Mexico, wrapped with cuttings of the host plant and occasionally small, infested, rooted plants from the field, and brought into quarantine at ARC-PPRI, Pretoria, from 1989 onwards (Craemer 1993). Laboratory and glasshouse cultures of *A. lantanae* developed on growing cuttings of the source plants, and were subsequently transferred to South African varieties of *L. camara* (*s.l.*). The cultures had to be destroyed and restarted several times, due to severe contamination by glasshouse pests such as mealybugs, which were eventually managed by rigorous manual control.

Aceria lantanae feeds and reproduces within the developing gall. Reproduction in eriophyids is by spermatophore transfer and arrhenotoky (Oldfield & Michalska 1996). Eriophyids double their populations in about 10 days (Sabelis & Bruin 1996). After multiplication within the gall, *A. lantanae* enters a dispersal phase during which it swarms on the gall surface. During this phase the

mites raise themselves on their anal lobes and caudal setae and claw the air with their two pairs of forelegs with four-rayed feather claws, which presumably aids dispersal. Eriophyid dispersal is normally by wind and by phoresy on flower-visiting insects (Sabelis & Bruin 1996).

The host range of *A. lantanae* in the native home comprises at least four *Lantana* spp. in section *Camara* (Palmer & Pullen 1995). Host-specificity tests on *A. lantanae* from Florida, U.S.A., in quarantine in Pretoria confirmed that the mite is essentially specific to *Lantana* sect. *Camara*. Indigenous African *Lantana* spp., which are all in the section *Calliorea*s (Day *et al.* 2003), *Lippia* spp. and other Verbenaceae were found to be totally resistant (Urban *et al.* 2001b; Mpedi & Urban 2003; Urban *et al.* 2004). The occasional induction by *A. lantanae* of very sparse, small, short-lived galls on Mexican *Lippia alba* (Mill.) plants in quarantine (Mpedi & Urban 2010) may indicate the closer relationship of Neotropical *Lippia* spp. than Afrotropical *Lippia* spp. to Neotropical *Lantana* spp.

Reduction in flowering of *L. camara* (*s.l.*) in quarantine was 0–96 %, depending on the lantana variety, with Australian varieties on average showing greater resistance to *A. lantanae* (Mpedi & Urban 2003; Urban *et al.* 2004).

Aceria lantanae can also feed on, deform and stunt vegetative growth of lantana (Craemer & Nesar 1990). Some of the leaf deformities resemble hormone herbicide damage, and are possibly caused by a hormone-mimicking chemical present in the saliva injected by the mite. No viruses or phytoplasmas were found in the deformed leaves (G. Kasdorf & G. Pietersen, pers. comm.).

Permission to release *A. lantanae* into South Africa was granted in 2007. The mite was released in mature lantana flower galls of approximately 10–20 mm diameter tied near the apex of flowering shoots, after removing buds, flowers and fruits to induce the production of new flowerbuds. *Aceria lantanae* established well on certain varieties of lantana especially under humid, frost-free conditions (Smith *et al.* 2010; Urban *et al.* 2011). Exposed stages and vagrant species of eriophyids are preyed upon by predatory mites (Acari), especially phytoseiids (Sabelis 1996), stigmatheids (Thistlewood *et al.* 1996) and tydaeids (Perring & McMurtry 1996). Numerous species of predatory mites are present on lantana (Walter 1999), but they do not prevent establishment of *A. lantanae*. *Aceria lantanae* successfully colonized lantana

Table 1. Development of biological control agents for *Lantana camara* L. (*sensu lato*) in South Africa during 1987–2010.

Candidate agent	Family	Feeding niche, mode	Status
Found suitable			
<i>Aceria lantanae</i>	Eriophyidae	Flower galler	Major, some varieties, humid
<i>Coelocephalopion camarae</i>	Brentidae	Petiole galler	Initial establishment
<i>Falconia intermedia</i>	Miridae	Leaf sucker	Localized establishment
<i>Longitarsus bethae</i>	Chrysomelidae	Root chewer	Initial establishment
<i>Ophiomyia camarae</i>	Agromyzidae	Leaf miner	Major, all varieties, humid
<i>Orthonama ignifera</i>	Geometridae	Leaf chewer	Must re-collect, Americas
<i>Passalora</i> (= <i>Mycovellosiella</i>) <i>lantanae</i> var. <i>lantanae</i>	Mycospherellaceae	Leaf spot pathogen	Did not establish
Rejected internally			
<i>Aconophora compressa</i>	Membracidae	Stem sucker	Insufficient specificity
<i>Aerenicopsis championi</i>	Cerambycidae	Stem borer	Cannot breed on lantana
<i>Aerenicopsis irumuara</i>	Cerambycidae	Stem borer	Cannot breed on lantana
<i>Alagoasa decemguttata</i>	Chrysomelidae	Leaf chewer	Insufficient specificity
<i>Alagoasa extrema</i>	Chrysomelidae	Leaf chewer	Insufficient specificity
<i>Asphondylia camarae</i>	Cecidomyiidae	Flower galler	Cannot breed on lantana?
<i>Barela parvisaccata</i>	Cicadellidae	Leaf sucker	Insufficient specificity
<i>Charidotis pygmaea</i>	Chrysomelidae	Leaf chewer	Insufficient specificity
<i>Eutreta xanthochaeta</i>	Tephritidae	Stem galler	Insufficient specificity
<i>Macugonalia geographica</i>	Cicadellidae	Stem sucker	Insufficient specificity
<i>Omophoita albicollis</i>	Chrysomelidae	Leaf chewer	Insufficient specificity
<i>Prospodium tuberculatum</i> isolate IMI 383461	Uropyxidaceae	Leaf rust	No susceptible South African lantana varieties
<i>Pseudanthonomus canescens</i>	Curculionidae	Flower miner	Insufficient specificity (?)
<i>Pseudanthonomus griseipilis</i>	Curculionidae	Flower miner	Insufficient specificity
<i>Septoria</i> sp.	Mycospherellaceae	Leaf spot pathogen	No susceptible South African lantana varieties
Shelved			
<i>Leptostales cf. hepaticaria</i>	Geometridae	Leaf chewer	Congener first
<i>Longitarsus columbicus columbicus</i>	Chrysomelidae	Root chewer	Congener first
<i>Longitarsus howdeni</i>	Chrysomelidae	Root chewer	Congener first
<i>Longitarsus</i> spp.	Chrysomelidae	Root chewers	Congener first
<i>Phenacoccus madeirensis</i>	Pseudococcidae	Stem sucker	Host-plant biotype (?)
<i>Teleonemia vulgata</i>	Tingidae	Leaf sucker	Host specificity (?)
Under investigation			
<i>Puccinia lantanae</i> isolate IMI 398849	Pucciniaceae	Leaf and stem rust	Pathogenic and virulent; host-specificity testing

infestations up to 50 km from the closest release sites within approximately two years (Urban *et al.* 2011). Flower galling by *A. lantanae* reduces seed production of susceptible lantana varieties along the humid coast of KZN by at least 85 % (Urban *et al.* 2011). The mite does not gall non-target plants in the field. *Aceria lantanae* was found to present no risk to indigenous Australian plants in quarantine in Pretoria (Mpedi & Urban 2005, 2010;

Urban *et al.* 2011), and, consequently, it has been exported to Australia.

Aconophora compressa Walker (Hemiptera: Membracidae)

To attack the under-utilized stem niche, a treehopper, *A. compressa*, was imported from the Alan Fletcher Research Station (AFRS), Australia, in 1995, for initial tests, from a culture started

with material from *L. urticifolia* (now known to be *L. camara* L.) in Mexico and Guatemala. It was re-collected from *camara*-like *Lantana* in Guatemala in 1997. Feeding by this gregarious stem sucker causes dieback of stems. It was rejected in South Africa due to its preference for and sustained breeding on indigenous African *Lippia* spp. (Heystek & Baars 2001, 2005). It was released into Australia, where it causes dieback of lantana stems. However, it bred more vigorously and was more damaging on the exotic, ornamental, fiddle-wood tree, *Citharexylum spinosum* L. (Verbenaceae) (Dhileepan *et al.* 2006), and also maintained field populations on several other non-target species, including the indigenous mangrove, *Avicennia marina* (Forssk.) Vierh. (Avicenniaceae) (Snow & Dhileepan 2008). Neither *C. spinosum* nor *A. marina* had been included among the test plants (Palmer *et al.* 2010). This case illustrates the importance of exposing the candidate agent in host-specificity tests in quarantine, not only to as many genera and species as practicable, in the family of the target weed, that are indigenous to the potential area of introduction, but also to closely-related economically or environmentally important plants.

Aerenicopsis championi Bates
(Coleoptera: Cerambycidae)

Larvae of *A. championi* were collected in bored stems of *L. ?camara* L. in Mexico in 1997. When implanted into detached sections of stems, or living stems of South African *L. camara* (*s.l.*), they bored actively downwards, making a series of holes through which they ejected frass, so that the distal part of the stem tended to break off, as was observed in the field. This candidate is impressively damaging, but adults were not obtained from living lantana plants in the laboratory. It also did not establish on weedy lantana, either in Hawaii (Day *et al.* 2003a) or in Australia (Day & Zalucki 2009), despite repeated releases in large numbers. This candidate therefore appears to be unable to breed sustainably on *L. camara* (*s.l.*).

Aerenicopsis irumuara Martins & Galileo
(Coleoptera: Cerambycidae)

Cerambycid larvae and pupae were collected in V-notched stems of *L. ?camara* L. in Guatemala in two batches in October 2002 and April 2004, and imported into quarantine in South Africa. They were described as a new species, *A. irumuara* (Martins & Galileo 2004). The adults oviposit near

the shoot-tip, and the larvae bore down the stem, making a series of holes through which they eject frass, gradually killing the stem.

Nearly 50 % of the medium-sized larvae collected in October 2002 bred through to adults in quarantine on cut sections of stems of South African varieties of weedy lantana. However, the females oviposited infrequently on *L. camara* (*s.l.*) in quarantine. The first batch could not be cultured, apparently because of excessive egg and neonatal larval mortality due to damage to the shoot tips of the plants by *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae), which was present as a contaminant (Mabuda 2004).

Multi-choice host-specificity tests were conducted with available adults from the second batch, in which the adults showed infrequent oviposition on lantana variety 009LP and 85 % as much oviposition on indigenous, African *Lippia* sp. B. There was continuous mortality of larvae on both these species, as well as on *Lantana rugosa* Thunb. and *Lippia rehmannii* H. Pearson, with survival after six months being 32 % on *L. camara* (*s.l.*) and 8 % on *Lippia* sp. B. The few adults obtained lived a maximum of two days, and a culture could not be maintained (Mabuda 2004). This candidate appears to be unable to breed sustainably on weedy lantana.

Alagoasa decemguttata (Fabricius)
(Coleoptera: Chrysomelidae: Galerucinae – formerly Alticinae)

The flea-beetle, *A. decemguttata* was collected from *camara*-like *Lantana* in Brazil during 1997. In a quarantine glasshouse, adults and larvae fed on the leaves of *L. camara* (*s.l.*) as well as on various other plant species in the Verbenaceae and Lamiaceae (H.E. Williams, unpubl.). Its host range is reported to include *Buddleja* species (Buddlejaceae) and many other plants (Begossi & Benson 1988). Insufficient specificity necessitated rejection of this candidate agent.

Alagoasa extrema (Harold)
(Coleoptera: Chrysomelidae: Galerucinae – formerly Alticinae)

The leaf-feeding flea-beetle, *A. extrema*, was collected from *Lantana ?camara* in southern Mexico in 1997 and 1998 because it appeared to be quite damaging, and aposematic alticines are often resistant to predation. The adults are trimorphic, producing all three colour forms from a single

egg-packet. Eggs are laid on the soil at the base of a host plant. Larvae feed on the leaves for about 2.5 weeks, and pupate in the soil. There is a three-fold range in performance on different varieties of *L. camara* (*s.l.*) (Williams 2006). Larval feeding reduces the above-ground biomass of the most-preferred lantana variety tested by up to 28 % (Williams 2005). This candidate was found to have many desirable characteristics, being not only voracious, but also fecund (laying seven eggs per day), multivoltine, and long-lived (>10 months). It was rejected internally because the indigenous African *Lippia rehmannii* and *Lippia* 'sp. B' (which may be a variant of the same species) (E. Retief, pers. comm.) were found to be 62 % and 72 % as suitable, respectively, as *L. camara* (*s.l.*) (Williams 2002; Williams & Duckett 2005). As its host range appeared to be restricted to the genera *Lantana* and *Lippia*, this candidate was considered likely to be suitable for use in Australia (Williams & Hill 2004).

However, *A. extrema* was also rejected in Australia because several generations were sustained on lemon verbena, *Aloysia triphylla* (L'Hér.) Britton (Verbenaceae), which is grown commercially, and there was complete development on eight other species in other genera (M.D. Day, pers. comm.). The apparent risk to lemon verbena in Australia was magnified unnaturally by using no-choice conditions in the tests. The actual risk to lemon verbena under naturalistic, multi-choice conditions in South Africa was <0.1 % of that of the most preferred variety of *L. camara* (*s.l.*) (Williams & Duckett 2005). This demonstrates the importance of using naturalistic test conditions, and appropriate criteria of suitability, to avoid unnecessary rejection of suitable candidates.

Asphondylia camarae Mohn (Diptera: Cecidomyiidae)

Asphondylia camarae was collected from *Lantana* ?*hirsuta* on the central highlands of Mexico in 2000, and *camara*-like *Lantana* spp. in Guatemala in 2002 and 2004. The lantana flower gall midge (and/or its associated fungus) induces the formation of 'gooseberry galls' in place of inflorescences. Attempts to breed the gall-midge on *L. camara* (*s.l.*) in quarantine were unsuccessful.

Barela parvisaccata Young

The leafhopper, *B. parvisaccata*, was collected from *Lantana* spp. in the arid north of the central

highlands of Mexico in 2000, an area with a climate comparable to the highveld region of South Africa to which most current lantana agents are poorly adapted. It was identified by P.H. Freytag (M. Stiller, pers. comm.). Adult females oviposit into the shoot-tips. Nymphal and adult feeding damage causes chlorotic speckling of the leaves, which presumably stunts both vegetative growth and reproductive output of the plant. It was hoped that this leafhopper would be able to survive periods of leaflessness of lantana, as eggs in the shoot-tips. This expectation became irrelevant when *B. parvisaccata* was found to breed faster on indigenous, African *Lippia scaberrima* Sond. than on the target weed, and it was rejected (Phenye & Simelane 2005). It was recommended as potentially suitable and valuable for Australia, but was declined in order to give priority to other candidates (M.D. Day, pers. comm.).

Charidotis pygmaea (Klug)

(Coleoptera: Chrysomelidae: Cassidinae)

The golden tortoise beetle, *Charidotis pygmaea*, was collected for AFRS by a contractor in southern Brazil, from a plant initially thought to be *L. tiliaefolia* [sic] Cham. (Swarbrick *et al.* 1998). It was imported from AFRS in 1994 for evaluation in South Africa. The entire life cycle is spent on the leaf lamina (Baars & Naser 1999).

In quarantine, it bred very poorly on *L. camara* (*s.l.*), and performed better on the indigenous, African *L. rugosa*, and especially on the South American creeping lantana, *L. montevidensis* (Spreng.) Briq., both of which are in section *Calliorea*s. The Brazilian source plant was subsequently found to be *L. fucata* Lindley, which is also in section *Calliorea*s (Day *et al.* 2003a). This candidate was culled in quarantine because it would be ineffective against *L. camara* (*s.l.*), and posed an unacceptable risk to the indigenous *L. rugosa* and the commercially used, non-invasive, exotic ornamental, *L. montevidensis* (Williams 2004).

Coelocephalopion camarae Kissinger (Coleoptera: Brentidae: Apioninae – formerly Apionidae)

Adults of the lantana petiole-galling weevil, *C. camarae*, were collected from *camara*-like *Lantana* taxa on the east and west coasts of central Mexico in 1997 and 2000 respectively. It was described as a new species (Kissinger 2000).

The adults are small (2–3 mm in length), black,

active, able to fly (Baars *et al.* 2007), and drop off the plant if disturbed. Adults chew small 'shot-holes' into the leaves, mainly alongside veins. The female usually lays each egg into the petiole, (Baars & Naser 1999; Baars *et al.* 2007) but occasionally into the midrib of leaves of all ages, or into the peduncle. The larva burrows inside the petiole and causes a small gall to form. Here the larva chews the vascular tissue in the petiole, disrupting transportation of water and photosynthates to and from the leaf. Leaves with galled petioles often wilt and die prematurely (Baars, *et al.* 2007). The mature larva pupates in the gall, and the adult emerges by chewing a small hole in the gall. The duration of the life cycle from egg to adult is about 35 days in the summer months. The female lays about one egg per day. Adults live for about five months and overwinter by sheltering in crevices on the plant and in the leaf litter (Baars & Naser 1999; Baars *et al.* 2007).

The weevil was found to be suitably host specific, during laboratory no-choice, paired-choice and multiple-choice tests. Under naturalistic multi-choice conditions, utilization of *Lippia* species was less than 7.6 % of that of *L. camara* (*s.l.*) (Baars 2000a). Females select petioles in excess of 1.5 mm in diameter for oviposition, a requirement that is not met in most of the related indigenous plants that were tested (Baars 2000a, 2002a). In multi-choice trials in the laboratory, *C. camararum* oviposited more on some lantana varieties than others, but there was no difference in the number of adult progeny produced (Baars & Heystek 2001; Baars 2002a).

Gall formation creates a nutrient sink, by effectively isolating the leaf and redirecting nutrients to the insect rather than to the growing parts of the plant. During impact studies in the laboratory, when 18 % of leaves were galled, root growth ceased (Baars *et al.* 2007). Galling of leaves therefore reduces the growth vigour and competitiveness of lantana.

Based on the insect's biology, host specificity and potential to inflict damage on the target weed, permission was granted for its release, and the first releases took place from October 2007 (Heystek 2007). Eleven releases were made on different varieties of weedy lantana at seven sites. At high altitudes there was no galling on two varieties, at mid altitudes there was only initial galling on two other varieties, and at the coast there has been establishment for three years to date on a single

variety at a single site. Populations of *C. camararum* at Richards Bay, KZN, reached 9 % of petioles galled in autumn 2009 (Heystek & Kistensamy 2009). Mass-rearing for release is continuing at ARC-PPRI and at the South African Sugar Research Institute (SASRI) near Durban.

Eutreta xanthochaeta Aldrich (Diptera: Tephritidae)

Another candidate that damages stems, the shoot-galling fruit-fly, *E. xanthochaeta*, had been released in small numbers in South Africa, after testing done in Australia, without establishment (Cilliers & Naser 1991). It was re-evaluated, to test the susceptibility of indigenous, African verbenaceous plants. Galled stems of *L. camara* (*s.l.*) were supplied by the Department of Agriculture, Hawaii, in 2003. Under naturalistic, multi-choice conditions, the fly oviposited on, and developed in, all indigenous, African *Lantana* and *Lippia* species that were tested, to approximately the same extent as on the reference variety of *L. camara* (*s.l.*). Populations on these non-target species were also shown to be sustainable for at least three generations under no-choice conditions. This candidate was therefore rejected as unsuitable for release into Africa (Mabuda 2005).

Falconia intermedia (Distant) (Hemiptera: Miridae)

Adults of the lantana mirid, *F. intermedia*, were collected from a *camara*-like *Lantana* plant in a garden in Jamaica in 1994 (Baars 2000b, 2001b; Baars *et al.* 2003), although it was also seen on wild *L. ?camara* L. in the field (J-R. Baars, pers. obs.). The adults are approximately 4 mm long, nearly black with transparent wings, move around actively when disturbed, and will take flight when repeatedly disturbed. They feed gregariously under leaves, causing visible white speckling on the upper leaf surface, and dark faecal spotting on the underside. Under heavy population pressure, the entire lamina turns white, followed by premature leaf abscission. Both chlorosis and defoliation reduce the photosynthetic capacity of the plants and repeated defoliation is a drain on their resources.

After a pre-oviposition period of 3–5 days, females lay eggs singly or in small batches, mostly along the margins on the underside of leaves. These hatch after 10–14 days. Five instars of highly mobile nymphs shelter mostly on the

underside of leaves. Development from egg to adult takes place in under a month in the laboratory in summer, and adults live for about two months (Heystek [sic] 2001; Baars *et al.* 2003).

Reproductive performance appeared not to be affected by the South African lantana variety, in a multiple-choice test at high population density (Baars 2000b, 2001b). However, in a no-choice test at low population density, there was a 15-fold range in reproductive performance on Australian lantana varieties, which ranged from highly resistant to highly susceptible, (Urban & Simelane 1999; Day & McAndrew 2003; Urban *et al.* 2004).

No-choice nymphal and adult performance trials indicated a limited host range, restricted to *L. camara* (s.l.) and indigenous *Lippia* spp. In multiple-choice trials, the assessed risk to the most susceptible non-target species was shown to be just less than 25 % (Baars *et al.* 2003). The marginal utilization of *Lippia* spp. was considered unlikely to be encountered under field conditions.

Based on its host specificity and potential to damage the target weed, permission was granted for the mirid's release. The first releases took place from April 1999 (Baars *et al.* 2003) in Pretoria and Tzaneen. An estimated 20 million mirids were mass-reared by ARC-PPRI and the mass-rearing stations of the *Working for Water* Programme (WfW) of the Department of Water Affairs, and released at over 80 sites throughout the weed's range in South Africa (Heystek & Olckers 2004). There was initial establishment of *F. intermedia* at 33 (41 %) of the release sites. Agent impact was measured in subtropical (LP, MP) and temperate (EC) areas. At peak impact in the subtropical area, *F. intermedia* reduced flowering by about 80 %, and defoliated some sites completely during the first three years (Heystek & Olckers 2004), whilst limited non-target effects were observed on *Lippia* species in close proximity to the weed (Heystek 2006). In the temperate area, impact was moderate, and waned over time (Heshula 2005; Heshula *et al.* 2005). Populations of this agent crashed countrywide, and it is currently only established at a few localized sites in the EC, MP and LP provinces.

Other factors, besides varietal resistance, which limited populations of *F. intermedia* were investigated. Ants were found to reduce the populations, but not eliminate them (F. Heystek, unpubl.; Tourle 2010). It was found that the waning of populations of *F. intermedia* could be ascribed to

the induction of resistance in lantana (Heshula 2009; Heshula & Hill 2009). *Falconia intermedia* was exported to AFRS in Australia, and was released widely from 2000 (Taylor *et al.* 2008), but has established only at a few sites in northern Queensland (Day & Zalucki 2009).

Leptostales cf. *hepaticaria* Guenée (Lepidoptera: Geometridae)

Larvae of a moth tentatively identified as *Leptostales* cf. *hepaticaria* were collected from *camara*-like *Lantana* spp. in Mexico in 1998. After rearing adult specimens for identification, further work on this candidate was shelved to give priority to another geometrid, *Orthonama ignifera* (Warren).

Longitarsus bethae Savini & Escalona (Coleoptera: Chrysomelidae: Galerucinae – formerly Alticinae)

To target a niche not exploited by any of the previously introduced lantana biological control agents, a root-feeding flea-beetle was collected from *L. camara* in a botanical garden in Cuernavaca, Mexico in 2000 (Simelane 2005). It was described as a new species, *L. bethae* (Savini & Escalona 2005). Its biology and factors affecting its performance were studied by Simelane (2004, 2006a,b, 2007a,b). Adults chew through the epidermis of leaves and feed on the mesophyll tissue, producing a smattering of irregularly shaped lesions. Eggs are laid singly or in small clusters of up to four on the surface of the soil near the stem of the host plant. Larvae burrow through the soil and penetrate the rootlets, where they feed internally, excavating elongate tunnels. Larger larvae feed externally on the roots, and pupate in a cell lined with compacted soil particles close to the soil surface. The immature stages are susceptible to predation by ants.

Pre-release evaluation showed that *L. bethae* was safe for release, and that it was likely to significantly damage the target weed, while being able to survive under a variety of environmental conditions in its new range (Simelane 2006a,c, 2010). Following permission to release *L. bethae* into South Africa in 2007, approximately 20 000 adult beetles were released at 20 sites located in the provinces of KZN, MP, GP, LP and EC. Initial establishment was recorded during 2008 and 2009 at KZN sites, but the plants at these sites were later destroyed by human activity, e.g. felled, burnt or buried. There was no establishment in GP, and

only tenuous signs of initial establishment were found at most sites in LP, MP and EC. *Longitarsus bethae* is well established and spreading at a site in MP with groundwater seepage. Mass-rearing of *L. bethae* is in progress at the South African Sugar Research Institute (SASRI) and ARC-PPRI to enable further releases.

Longitarsus columbicus columbicus Harold
(Coleoptera: Chrysomelidae: Galerucinae – formerly Alticinae)

The root feeder, *L. columbicus columbicus*, was collected from a *Lantana* sp. in Venezuela in 1998 and cultured without difficulty in the laboratory. Its biology is similar to that of *L. bethae*, with mature larvae feeding externally on the roots, and immature stages also being susceptible to predation by ants. *Longitarsus columbicus* diapauses in winter, which may help the insect to bridge the dry season in South Africa. Its recorded host range in its native home is confined to *Lantana* spp. In the laboratory, there was no apparent difference in intensity of feeding damage, or number of progeny produced in the first and second generations, when *L. columbicus* was reared on eight of the dominant South African varieties of *L. camara* (*s.l.*) (Baars 2001a).

This candidate was shelved in order to give priority to its congener, *L. bethae*. Following the tenuous degree of establishment of *L. bethae* on weedy lantana in South Africa, and the apparently closer relationship of weedy lantana from Australia and South Africa to *Lantana* taxa from Venezuela rather than Mexico (Watts 2010), priority could be given to re-collecting *L. columbicus columbicus*, and evaluating its suitability for release.

Other *Longitarsus* spp.
(Coleoptera: Chrysomelidae: Galerucinae – formerly Alticinae)

Longitarsus howdeni (Blake) from Jamaica, and undetermined *Longitarsus* spp. collected from *Lantana* spp. in Florida, Cuba, Mexico and Trinidad, could not be reared readily in the laboratory (Baars 2001a) and were shelved while priority was given to their congener, *L. bethae*.

Macugonalia geographica (Signoret)

The stem-feeding leafhopper, *M. geographica*, was collected from *Lantana ?tiliifolia* in southern Brazil in 2002. It feeds voraciously on the xylem, and may therefore be damaging to drought-

stressed plants. After identification (M. Stiller, pers. comm.), it was found to be unsuitable because its host range includes citrus, coffee and grapevine, and it is considered a potential vector of the bacterium that causes Pierce's Disease (Ringenberg *et al.* 2010).

Omophoita albicollis (Fabricius)
(Coleoptera: Chrysomelidae: Galerucinae)

Omophoita albicollis was collected from *camara*-like *Lantana* spp. in Jamaica in 1993. Adults feed on the flowers and leaves and oviposit under leaf litter on the soil. Larvae feed on the lower leaves and pupate in the soil. Following identification of the candidate, it was found that its recorded hosts include *Stachytarpheta* spp. (Verbenaceae) and *Heliotropium* spp. (Boraginaceae) (Virkki *et al.* 1991). In multi-choice tests in quarantine, adults caused approximately equal amounts of feeding damage to *L. camara* (*s.l.*), indigenous African *Lippia* spp. and other plants in the Verbenaceae and Lamiaceae (H.E. Williams, unpubl.). Inadequate specificity necessitated candidate rejection (Baars & Nesar 1999).

Ophiomyia camararum Spencer
(Diptera: Agromyzidae)

The herringbone leaf-mining fly, *O. camararum*, known from Florida to the southeast coast of Brazil, was identified as a potential biological control agent for *L. camara* (*s.l.*) by Stegmaier (1966). It was collected from *L. camara* (*s.l.*) in Florida (U.S.A.) in 1997 for evaluation in quarantine in South Africa, and its biology and host specificity were studied by Simelane (2001, 2002a,b). The adult female inserts its eggs singly into the leaf tissue, often into a lateral vein. Upon hatching, the larva tunnels along the leaf veins, especially the midrib, which results in a mine with a herringbone pattern, often leading to leaf chlorosis and premature abscission.

The fly was found to be suitable for release against lantana, and permission for its release in South Africa was granted in 2001. Establishment of *O. camararum* in South Africa was confirmed following the release of approximately 15 000 pupae in leaves at 20 sites in five provinces during 2001 and 2002 (Simelane & Phenye 2004). Whilst *O. camararum* has flourished in the hot and humid, low altitude, coastal regions of KZN, Swaziland and Mozambique (Simelane & Phenye 2004; Urban & Phenye 2005), it remains relatively sparse in less humid,

higher altitude areas of MP, LP and Swaziland (Magagula 2010) and cannot overwinter on the highveld (GP and NW) where lantana becomes dormant and generally leafless in winter. *Ophiomyia camarar* has dispersed widely, with new populations being found recently in western Madagascar (Urban *et al.* 2010a), northeastern Tanzania (J. Coetzee, pers. comm.) and southern Ethiopia (Urban *et al.* 2010b).

In a semi-field impact study over six months, it was found that *O. camarar* starter populations of two densities built up rapidly to a similar plateau level that reduced lantana stem height and diameter, leaf and flower density, and above-ground biomass by 19 %, 28 %, 73 %, 99 % and 49 %, respectively (Simelane & Pheny 2005).

Ophiomyia camarar became one of the most abundant biological control agents on lantana in the humid coastal region of KZN, with damage recorded on up to 86 % of leaves per site (Urban & Pheny 2005). Heystek (2006) observed that coastal populations of the leaf-mining beetle, *Uroplata girardi* Pic (Coleoptera: Chrysomelidae: Cassidinae), crashed when *O. camarar* proliferated on the same variety of lantana in the same region, and he hypothesized that this was due to inter-specific competition between these agents. Competitive interaction between *O. camarar* and *U. girardi* was confirmed by cage and field studies (April 2009), but both agents coexist in the field, and the overall impact on lantana is considered to have increased.

Ophiomyia camarar was exported to AFRS in Brisbane, Australia, where it was released at 35 sites in 2007, and recovered at 12 in north and southeastern Queensland (Taylor *et al.* 2008; Day & Zalucki 2009). In 2008, a parasitoid-free colony of *O. camarar* was exported to the National Agricultural Research Organization in Kampala, Uganda, where adults were released into a sleeve-cage on lantana but did not establish (R. Molo, pers. comm.). Other adults from this consignment may have dispersed 670 km southeast and 840 km northeast in about 18 months to the recovery sites in Tanzania and Ethiopia.

Orthonama ignifera (Warren)
(Lepidoptera: Geometridae)

Larvae of *O. ignifera* [formerly in *Leptostales*] were collected from *camara*-like *Lantana* taxa in subtropical Florida, U.S.A., in 1996, and Mexico in 1998. The adult moths are reddish brown with a distinctive,

wavy, orange-red stripe along the outer edges of the forewings. The females lay eggs singly on the leaves and stems of the host plant. The larvae are brownish grey and can cause extensive damage while feeding on the underside of the leaves.

Orthonama ignifera has a short life cycle. The pre-oviposition period is 1–2 days and the egg stage lasts 2–6 days. The five larval instars take 17–24 days. Adult males and females live 2–10 days, and females lay between 16 and 105 eggs (Williams & Madire 2008).

In larval no-choice trials in a quarantine glasshouse, larval development occurred on nine out of the 28 plant species tested (Williams & Madire 2008). Larval survival on these test plants was comparable to that on the control variety of lantana, but female pupal mass was significantly less. Plants that supported larval development were exposed to adults in a 3 × 4 lattice in multi-choice trials in a walk-in cage. Females selected *L. camara* (*s.l.*) strongly for oviposition, in preference to *Lippia* spp. A risk analysis (Wan & Harris 1997), which calculated the product of the proportional rates of oviposition and development on non-target species compared to that on a reference variety of the target weed, *L. camara* (*s.l.*), showed that the risk to all non-target species was less than 4 %, confirming that *O. ignifera* is suitable for release into Africa (Williams & Madire 2008). Clearance to release was granted, but the laboratory colony died out before any releases could be made, and the moth will have to be re-collected from the New World before it can be released.

Passalora lantanae (Chupp) U. Braun & Crous
var. *lantanae*
(Mycosporrellales: Mycosporrellaceae)

An anamorphic fungus, *P. lantanae* var. *lantanae* (formerly *Mycovellosiella lantanae* (Chupp) Deighton var. *lantanae*), was first noted by Deighton (1974) to occur on various *L. camara* plants in Brazil, Puerto Rico and Venezuela. Several brief field surveys by ARC-PPRI staff to South and Central America between 1987 and 1997, along with research and observations by Evans (1987) and Barreto *et al.* (1995), led to this fungus being selected as the most promising, potential, fungal biological control agent for lantana in South Africa (Morris *et al.* 1999; den Breejen & Morris 2003). An isolate was collected from *L. camara* (*s.l.*) in Florida, U.S.A., and cultured in quarantine in South Africa, where it was found to be host-specific to certain

biotypes of lantana. Additional isolates were tested with a view to broadening the range of pathogenicity to South African varieties of lantana (Morris *et al.* 1999; den Breeÿen & Morris 2003).

Permission to release *P. lantanae* var. *lantanae* was granted in September 2001 (den Breeÿen 2003). Releases were made in EC, KZN and MP provinces with a combination of the three most virulent isolates formulated as an aqueous spore suspension and an oil-based spore suspension (den Breeÿen 2003). Although symptoms were observed on lantana within the first three months of release, the fungus did not persist (Retief 2010a), possibly because it could not bridge the dry winter season. *Passalora lantanae* var. *lantanae* is also not amenable to use as a mycoherbicide (den Breeÿen 2003), and has been rejected in favour of other pathogenic fungi.

Phenacoccus madeirensis Green
(Hemiptera: Pseudococcidae)

A stem-sucking pseudococcid appeared to be killing beds of horticultural *L. camara* (*s.l.*) in Brazil in 2002. The insect was identified (I.A. Millar, pers. comm.) as *P. madeirensis*, a polyphagous plant pest, already present and recorded from lantana in South Africa. The same species was found to be locally common and slightly damaging on weedy lantana in Tanzania (S. Nesor, pers. comm.), and in Ghana, where it killed lantana in some regions (Scheibelreiter 1980). This suggests that there may be a virulent, lantana-preferring biotype of *P. madeirensis*, and consideration could perhaps be given to researching whether or not there is a sufficiently lantana-specific biotype for use against *L. camara* (*s.l.*). However, *P. madeirensis* on lantana in South Africa is heavily parasitized, mainly by *Anagyris* sp. near *agraensis* Sarawat (Hymenoptera: Encyrtidae).

Prospodium tuberculatum (Speg.) Arthur
(Pucciniales: Uropyxidaceae)

A number of fungal pathogens have been recorded on *L. camara* in the Neotropical Region (Evans 1987; Barreto *et al.* 1995; Thomas & Ellison 2000). The rust fungus, *P. tuberculatum*, was observed to cause extensive necrosis on leaves in Brazil, Argentina, Jamaica and Mexico, where it is considered to be one of the most damaging fungi on lantana (Evans 1987). Isolate IMI 383461 of *P. tuberculatum*, collected in Brazil and tested by CABI Europe-U.K., was found to be host-specific

to *L. camara* (*s.l.*) (Thomas *et al.* 2006). This isolate infects only some pink varieties of lantana in Australia (Day *et al.* 2003b), but both pink and orange varieties from New Zealand are moderately susceptible (Waipara *et al.* 2009). It requires subtropical summer conditions for infection (Ellison *et al.* 2006). It produces urediniospores relatively quickly, and is dispersed by wind. It also produces teliospores (Ellison *et al.* 2006), giving the fungus the ability to survive the dry winter months. It was released in Australia in 2001 for classical biological control.

In preliminary testing by CABI, six South African varieties of *L. camara* (*s.l.*) were found not to support complete development of *P. tuberculatum* (Thomas & Ellison 1999). Microscopic examination revealed that *P. tuberculatum* was able to germinate on the plant surface but was unable to develop further (Thomas & Ellison 1999). Following its establishment in Australia, persistence through several successive years of drought, and re-emergence during a subsequent wet season (M.D. Day, pers. comm.), it was decided to import this isolate from Queensland to test its pathogenicity to additional South African varieties of lantana.

Cuttings of a susceptible lantana variety, Brisbane common pink, were imported into South Africa from AFRS in 2009, followed by the fungus, to establish an *in vivo* culture of the rust. During pathogenicity testing, three plants of each biotype were inoculated with urediniospores of *P. tuberculatum* according to the method of Ellison *et al.* (2006). A Brisbane common pink plant was included with each test as a control. All inoculated plants were observed for four weeks after sporulation had occurred on the control plants, to allow for the development of any latent infections. Macroscopic symptoms were recorded during this time, and leaf sections were collected from each inoculated plant and placed in a leaf-clearing and staining solution to investigate the host and non-host responses microscopically.

In each test run, rust pustules (uredinia) developed normally on the Brisbane common pink lantana variety, but on none of the 26 South African lantana varieties tested. The only macroscopic symptom observed on some of the varieties was a faint yellow discolouration on the upper surface of the inoculated leaves. Microscopic examination of the leaves revealed a resistance response in all varieties. In each case, the spores germinated and there was normal appressorium development

over the stomata. However, no penetration occurred and a brown stain could be observed underneath the stomata, indicating a hypersensitive reaction of the leaf to the rust inoculum. This confirmation that the fungus is non-pathogenic to South African varieties of lantana led to its rejection (Retief 2010b).

Pseudanthonomus canescens Faust
(Coleoptera: Curculionidae)

To increase the levels of damage inflicted on the reproductive structures of lantana, two flower-mining curculionids of the genus *Pseudanthonomus* were imported for evaluation in quarantine at the ARC-PPRI laboratories in Pretoria. Material of the first species was collected from an orange-flowered *camara*-like *Lantana* species in Brazil in 2002, and bred (see below) on detached inflorescences of *L. camara* (*s.l.*) This provenance was identified as *P. canescens* (W.E. Clark, pers. comm.), a species with a distribution range which extends from Argentina to Venezuela, and with adults that have been collected not only from *L. camara* in Uruguay and Trinidad but also from *Lippia alba* in Venezuela, and from food (not necessarily host) plants in the Caprifoliaceae and Malvaceae (Clark 1990). Because it is probably not sufficiently host specific, and due to the laboriousness of breeding it in captivity, it was rejected.

Pseudanthonomus griseipilis Champion
(Coleoptera: Curculionidae)

The second flower-mining weevil, *P. griseipilis*, has been recorded only from *L. camara* in Columbia, Costa Rica, El Salvador and Honduras (Clark 1990). It was collected from an orange-flowered *camara*-like *Lantana* species in Guatemala during 2002. The adults oviposit into flowerbuds. As the developing larvae cause the flowers of *L. camara* (*s.l.*) to abort prematurely in the glasshouse, the insects were reared by laboriously transplanting partly developed larvae into lantana inflorescence receptacles.

During a series of multi-choice tests in quarantine, using arrays of inflorescences, adults of *P. griseipilis* frequently oviposited on indigenous African *L. rugosa* and the introduced, horticultural *L. montevidensis*, both of which are in *Lantana* sect. *Callioreas*, as well as occasionally on indigenous African *Lippia* spp., in which the progeny also completed their development (F. Heystek & Y. Kistensamy, unpubl.). This candidate was therefore rejected as being insufficiently host-specific.

Puccinia lantanae Farl.
(Pucciniales: Pucciniaceae)

The rust, *P. lantanae* was recorded on *L. camara* in Brazil, Venezuela and the West Indies (Evans 1987) and is also known from Mexico. Pathologists of CABI Europe-U.K. collected *P. lantanae* isolate IMI 398849 from the Amazonian region of Peru and found it to be pathogenic to a wider range of weedy lantana varieties than *P. tuberculatum*, and to attack the stems as well as the leaves (Thomas & Ellison 2000). Three out of five lantana biotypes from South Africa were found to be susceptible to this isolate (Thomas & Ellison 1999). A contractual agreement has been made with CABI Europe-U.K. to conduct research on this pathogen, which mainly involves testing the susceptibility of some non-target plants of importance to Africa to this specific isolate of *P. lantanae*.

If the fungus is found to pose no significant risk to the non-target plants tested, CABI will supply ARC-PPRI with the pathogen for further testing in quarantine. Parallel investigations are being undertaken by CABI for Australia. This candidate may be suitably host-specific, because it is non-pathogenic to *Lantana montevidensis* (Spreng.) Briq. section *Callioreas* (Renteria B. & Ellison 2004).

Septoria sp.
(Mycosphaerellales: Mycosphaerellaceae)

An anamorphic fungus, *Septoria* sp., was collected from Ecuador and found to be pathogenic to *L. camara* (*s.l.*) in Hawaii (Trujillo & Norman 1995). It was released in Hawaii during 1997 and established successfully in the forest on Kauai Island (Trujillo 1997). *Septoria lantanae* Garman was first described by Garman (1915) from *L. camara* leaves in Puerto Rico. However, the morphological features of the *Septoria* sp. isolated from Ecuador do not fit those described for *S. lantanae*, and the fungus under investigation may be a different species. Leaves infected with *Septoria* sp. were collected by E. Trujillo from *L. camara* (*s.l.*) on Kauai Island and sent to the quarantine facilities at the ARC-PPRI, Stellenbosch. The pathogen was isolated into pure *in vitro* culture on agar by removing spores from the spore-bearing pycnidia which occurred on the surface of the leaf lesions. Seven of the major South African varieties of *L. camara* (*s.l.*) were tested and found not to be susceptible to *Septoria* sp. Several more lantana varieties have been collected to test whether they may be

genetically closer to the susceptible Hawaiian variety of lantana, and pathogenicity testing is ongoing.

Teleonemia vulgata Drake & Hambleton
(Hemiptera: Tingidae)

Teleonemia spp. are possibly the most widespread and common phytophages on *Lantana* spp. in Brazil, with some species coexisting in sympatry (Winder & Harley 1983). The leaf-sucking tingid, *T. vulgata*, was collected from *L. ?tiliifolia* in southern Brazil in 1996. It bred erratically on varieties of *L. camara* (*s.l.*) in quarantine, and caused considerable leaf chlorosis, but also developed well on indigenous, African *Lantana* and *Lippia* spp. In multi-choice tests in relatively small (140 × 123 × 93 cm) bench-top cages, in recirculating air, 28–45 % as many progeny emerged from three indigenous African *Lippia* species as from *L. camara* (*s.l.*), and this candidate was therefore shelved (Baars 2002b). It could be re-collected for testing under more naturalistic, multi-choice conditions in a much larger cage in a through-flow stream of fresh air.

CURRENT STATUS OF LANTANA BIOLOGICAL CONTROL IN SOUTH AFRICA

Lantana biological control agents and lantana-associated insects in South Africa

Earlier research in South Africa, aimed at biological control of lantana (Oosthuizen 1964; Cilliers 1987a; Cilliers & Nesar 1991) resulted in the establishment of five agents, *Calycomyza lantanae* (Frick) (Diptera: Agromyzidae), *Octotoma scabripennis* Guérin-Mèneville (Coleoptera: Chrysomelidae: Cassidinae – formerly Hispinae), *Salbia haemorrhoidalis* (Guenée) (Lepidoptera: Crambidae), *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae) and *Uroplata girardi* Pic (Coleoptera: Chrysomelidae: Cassidinae – formerly Hispinae), which were originally developed in Hawaii and imported from Hawaii or Australia. Their introduction was intended to complement seven other insect species already associated with lantana in South Africa, including three species thought to have been accidentally introduced with the host plant, namely *Crociosema lantana* (formerly in *Epinotia*) Busck (Lepidoptera: Tortricidae), *Lantanophaga pusillidactyla* (Walker) (Lepidoptera: Pterophoridae), and *Ophiomyia lantanae* (Froggatt) (Diptera: Agromyzidae), two indigenous, African

insects, *Aristaea onychota* Meyrick (Lepidoptera: Gracillariidae) and *Hypena laceratalis* Walker (Lepidoptera: Noctuidae) and two polyphagous pests, *Orthezia insignis* Browne, (Hemiptera: Ortheziidae) and *Phenacoccus parvus* Morrison (Hemiptera: Pseudococcidae) (Baars & Nesar 1999). Since then, six newly-developed lantana biological control agents (*A. lantanae*, *C. camarae*, *F. intermedia*, *L. bethae*, *O. camarae* and *P. lantanae* var. *lantanae*) have been introduced.

Predicting the outcome of introductions

Predictions, by biological-control practitioners, of a candidate agent's likelihood of successfully establishing, proliferating, and significantly suppressing the target weed, tend to be over-optimistic (D.J. Greathead, pers. comm.). This was verified by experience with the six newly-developed agents that have been released on lantana in South Africa since 1999. Whilst *O. camarae* performed better than predicted (Urban & Phenyne 2005), and *A. lantanae* more-or-less as predicted (Urban *et al.* 2010b; Urban & Mpedi 2010), the performance of four others, *F. intermedia* (Baars 2000b, 2001b, 2002a; Day & McAndrew 2003), *P. lantanae* var. *lantanae* (Evans 1987; Barreto *et al.* 1995; Morris *et al.* 1999), *C. camarae* (Baars & Heystek 2001; Baars 2002a; Baars *et al.* 2004) and *L. bethae* (Simelane 2004; 2005, 2006a, 2010), was overestimated. Performance is largely unpredictable: it remains to be seen whether the tenuous start made by the last two agents can be improved by expanded mass-rearing, and releasing in greater numbers.

Specificity realized in the field

Post-release monitoring of agent establishment and proliferation on *L. camara* (*s.l.*) includes scouting for impacts on non-target plants. Spillover of *F. intermedia* sometimes occurs, from well-infested lantana onto nearby *Lippia* spp., causing conspicuous chlorosis, which is related to the proximity of the *Lippia* spp. to *L. camara* (*s.l.*) (Heystek 2006). *Ophiomyia camarae*, which was shown to utilize *Lippia* spp. when paired with lantana in the laboratory, and increasingly under higher population pressure (Simelane 2002b), utilized less than 1 % of *Lippia* leaves whilst the agent was in outbreak population density in the field (Urban & Phenyne 2005). The initial 'scribbles' seen on *Lippia* spp. could equally well have been those of the indigenous, African leaf-mining moth, *A. onychota*, which, like *H. laceratalis*, colonized introduced

L. camara (s.l.) from its normal indigenous, African *Lantana* and *Lippia* host plants (Kroon 1999; Baars 2003). *Aceria lantanae* galls were not found on any non-target plants growing in close proximity to well-colonized *L. camara* (s.l.) (Urban *et al.* 2011).

Field surveys also showed, with one exception, that all the lantana biological control agents that had been introduced earlier were highly host-specific. The exception was *T. scrupulosa* which was often found on indigenous African *L. rugosa* and *Lippia* spp., especially when close to *L. camara* (s.l.) (Heystek 2006). *Teleonemia scrupulosa* is known not to be highly host-specific (Day *et al.* 2003a), and retrospective investigations of its host specificity showed that it would have been considered unsuitable for release, according to present-day criteria (Heystek 2006).

Distribution and abundance of established agents

Countrywide surveys in South Africa of the distribution and abundance of the biological control agents and lantana-associated insects established on lantana (Baars 2003; Baars & Heystek 2003; Heystek 2006) show that their populations are not uniformly distributed, and are sparse overall, averaging about 10 % of their potential density (Table 2). In Swaziland, the established biological control agents and lantana-associated insects are most abundant where rainfall is highest and plant condition is most favourable, but they are occasional to rare overall, as is their apparent impact on lantana (Magagula 2010).

Impact on *L. camara* L. (*sensu lato*)

Chemical exclusion studies using aldicarb demonstrated that the agents released earlier, *T. scrupulosa*, *O. scabripennis* and *U. girardi*, reduce the rates of growth and reproduction of lantana measurably on the coast of KZN (Cilliers 1987a,b). Intermittent outbreaks of these three agents have been observed in MP and KZN during the last few years, as well as an outbreak of *S. haemorrhoidalis* in LP. During these occurrences, localized but large stands of lantana were heavily defoliated.

Laboratory studies on the more-recently released agents showed that they all have the potential to reduce markedly the rate of growth and reproduction of lantana. Under outbreak densities in the field, *F. intermedia* caused massive chlorosis, defoliation, and reduction in flowering and fruiting (Baars 2001b; Heystek & Olckers 2004), but this

happened shortly after release only, and the agent has since become scarce or localized (Heshula 2005; Heshula *et al.* 2005). Semi-field studies (on caged plants growing in the ground) showed that *O. camarae* could approximately halve the growth and reproduction of lantana (Simelane & Phenyne 2005). Similar population densities to those in the field cages are reached each year along the coast of KZN, indicating that *O. camarae* is suppressing lantana markedly on an annual basis in that region (Urban & Phenyne 2005). Up to at least 85 % of flowerbuds are being galled by *A. lantanae* in the field, greatly reducing seeding, but only on some lantana varieties and only under humid, frost-free conditions (Urban *et al.* 2011). On small plants in the laboratory, shoot growth is halved and root growth halted when 18 % of petioles are galled by *C. camarae* (Baars *et al.* 2007), and this apionid has achieved 9 % galling at one coastal site. Growth and reproduction of lantana are markedly reduced by *L. bethae* under laboratory and semi-field conditions (Simelane 2010), but establishment in the field is limited to coastal or wetter sites and is tenuous at this stage. Mass-rearing of the last two agents has been expanded to make it possible to release greater numbers per site, in an effort to improve establishment, and ultimately impact.

Preparations are under way to measure the combined impact of all established lantana biological control agents by chemical exclusion on the coast of KZN, where impact is very marked, and in an inland area in MP, where their impact is typically far more limited.

CONSTRAINTS ON AGENT PROLIFERATION

In view of the generally low population density of most lantana biological control agents in most countries (Day *et al.* 2003a), the constraints on agent performance are often debated (Neser & Cilliers 1990; Cilliers & Neser 1991; Swarbrick *et al.* 1998; Baars & Neser 1999; Day & Neser 2000; Day *et al.* 2003a; Day & Zalucki 2009) and may act in combination, as on the recently released agents discussed below.

Climatic incompatibility

Disease symptoms were initially caused by *P. lantanae* var. *lantanae* on *L. camara* (s.l.) in the field in South Africa, but the fungus did not establish (Retief 2010a), possibly due to inability to cope with the dry season. All five of the recently released

Table 2. Relative abundance of biological control agents and lantana-associated insects on *Lantana camara* L. (*sensu lato*) in the lantana-infested provinces of South Africa, ex data of Heystek (2006). *Phenacoccus parvus*^b has been recorded at very low density in Gauteng only. *Passalora* (= *Mycovellosiella*) *lantanae* var. *lantanae* did not establish at any of the release sites in the three provinces in which it was released. Three agents were released after this survey: *Aceria lantanae* is now abundant on certain lantana varieties on the coast of KZN, and very scarce inland; *Coelocephalapion camarae* is established on the coast of KZN only; *Longitarsus bethae* has shown signs of initial establishment on the coast of KZN only.

<i>Lantana camara</i> biological control agent or lantana-associated insect	Relative abundance (% of maximum possible) at <i>n</i> sites in the South African province							Mean
	WC ^c <i>n</i> = 6	EC <i>n</i> = 30	KZ <i>n</i> = 14	MP <i>n</i> = 16	LP <i>n</i> = 7	NW <i>n</i> = 5	GP <i>n</i> = 3	
<i>Aristaea onychota</i> ^a	0	5	7	8	7	17	11	7.9
<i>Calycomyza lantanae</i>	5	33	38	18	22	29	15	22.9
<i>Crociosema lantana</i>	7	22	5	9	6	5	1	7.9
<i>Falconia intermedia</i>	0	11	0	2	2	0	0	2.1
<i>Hypena laceratalis</i> ^a	18	43	20	29	26	35	14	26.4
<i>Lantanophaga pusillidactyla</i>	0	4	0	2	1	4	2	1.9
<i>Octotoma scabripennis</i>	0	2	2	7	5	5	0	3.0
<i>Ophiomyia camarae</i>	0	10	42	12	7	0	0	10.1
<i>Ophiomyia lantanae</i>	20	23	14	22	19	20	1	17.0
<i>Orthezia insignis</i> ^b	0	2	16	3	6	0	0	3.9
<i>Salbia haemorrhoidalis</i>	0	5	6	5	2	0	0	2.6
<i>Teleonemia scrupulosa</i>	16	17	10	11	5	35	17	15.9
<i>Uroplata girardi</i>	0	0	7	0	0	0	0	1.0
Mean	5.1	13.6	12.8	9.8	8.3	11.5	4.7	9.4

^aIndigenous to Africa.

^bPolyphagous pest with preference for lantana.

^cProvinces: EC, Eastern Cape; GP, Gauteng; KZ, KwaZulu-Natal; LP, Limpopo; MP, Mpumalanga; NW, North West; WC, Western Cape.

agents that did establish, perform better under humid, coastal conditions or at wetter sites where plant condition is better. Recent outbreaks of *F. intermedia* have only been observed near the coast (EC). Whilst *O. camarae* remains abundant along the hot and humid coast of KZN in autumn, it is relatively sparse in a cooler coastal area (EC) and in the hot but less humid interior (MP, LP), and absent from the highveld (GP, NW) (Table 2). When the leaves of its host are killed by frost, the agent is deprived of a substrate for reproduction for too long a period for it to survive. The performance of *O. camarae* in Queensland is also related to heat and humidity (Day & Zalucki 2009). *Aceria lantanae* is prolific under hot and humid coastal conditions (Urban *et al.* 2011), and breeds well during a wet summer inland, but cannot survive frost. Although *U. girardi* had failed to establish on lantana in a dry area near Kitwe, Zambia (Löyttyneimi 1982), it thrived under rainforest conditions opposite Mosi-oa-Tunya/Victoria Falls when re-imported into Zambia in a cooperative

effort with CABI-Africa in 2009 (A.B.R. Witt, pers. comm.).

There is a clear need to develop new lantana biological control agents adapted to the more extreme, climatic conditions inland. Exploration on the central highlands of Mexico yielded the leafhopper, *B. parvisaccata*, the stem-inserted eggs of which may be able to bridge the cold, dry season. This candidate was found to be unsuitable for Africa, because it bred better on indigenous, African *Lippia scaberrima* than *L. camara* (*s.l.*) (Phenye & Simelane 2005), but it could be considered as a candidate for other parts of the world. Exploration for additional promising natural enemies should be directed towards areas having a continental climate with a dry winter.

Acquired predators and parasitoids

Generalist predators such as spiders and insectivorous birds, which are ubiquitous and common, undoubtedly consume exposed stages of phytophagous biological control agents and constrain

their effectiveness. Predation by ants on *F. intermedia* in the field was shown to delay defoliation of lantana (F. Heystek & Y. Kistensamy, unpubl.). In laboratory studies, foraging ants of two *Crematogaster* spp. (Hymenoptera: Formicidae) were shown to be significant predators of several lantana biological control agents, especially the smaller (≤ 10 mm) larvae of the externally-feeding noctuid, *H. laceratalis*, but also the mobile nymphs of the leaf-sucking mirid, *F. intermedia* and, somewhat less so, of the more-sedentary nymphs of the tingid, *T. scrupulosa* (Tourle 2010).

The herringbone leaf miner, *O. camarae*, has been colonized by indigenous, African parasitoids (Urban & Phenyne 2005), which could reduce the rate of annual population increase and the peak levels reached. The rich fauna of predatory mites on lantana (Walter 1999) may possibly do the same to the flower gall mite, *A. lantanae*. Despite acquiring natural enemies, however, both of these agents reach densities that seriously damage susceptible varieties of lantana in the most favourable climatic zone (Urban & Phenyne 2005; Urban *et al.* 2011).

Varietal resistance

Physical and chemical characteristics of different lantana varieties influence agent establishment and proliferation. The mirid, *F. intermedia*, showed a 15-fold range in rate of reproduction in no-choice tests on different Australian varieties of lantana under glasshouse conditions (Urban & Simelane 1999; Day & McAndrew 2003; Urban *et al.* 2004), and some lantana varieties, repeatedly inundated with large numbers of mirids in the field, were found to be totally resistant to this agent (W. Botha, pers. comm.). In the laboratory, the apionid, *C. camarae*, oviposited more heavily on lantana varieties with thicker leaf petioles (Baars *et al.* 2007). Larvae of the flea-beetle, *L. bethae*, developed about three times as well on some varieties of lantana as on others (Simelane 2006b). The agromyzid, *O. camarae*, is about twice as abundant on one lantana variety in the field as on other sympatric varieties (Heystek 2006). Lantana varieties range from highly susceptible to highly resistant to the eriophyid mite, *A. lantanae* (Urban *et al.* 2001b, 2004, 2011; Mpedi & Urban 2003). The possible role of allelochemicals and allopolyploidy in varietal resistance is discussed below.

As each agent utilizes a limited proportion of the large number of lantana varieties present, it is essential to introduce many agents and biotypes,

with complementary varietal preferences, to achieve adequate biological control of the whole array of weedy lantana taxa.

Induced resistance

Herbivory by phytophagous insects induces plants to produce physical structures and allelochemicals that confer resistance by inhibiting insect feeding, digestion or oviposition (Chen 2008). Pruning increases the toxicity of *Lippia* plants, presumably by inducing them to either translocate defensive chemicals from the roots to the shoots, or by increasing the biosynthesis of allelochemicals in the leaves (Roets 1937). The observation that individual trees of *C. spinosum* in Australia, that were initially heavily infested with *A. compressa*, supported very sparse populations in subsequent years (M.D. Day, pers. comm.), despite *A. compressa* maintaining high numbers on *L. camara* (*s.l.*), suggests possible induced resistance, but Manners & Walter (2009) considered plant condition to be the main factor limiting populations of *A. compressa*, and feeding on *C. spinosum* caused defoliation (M.D. Day, pers. comm.), which could have indirectly reduced insect populations. The pathogen, *P. tuberculatum*, induced a resistance response (hypersensitivity, *i.e.* the death of plant cells at the point of attempted fungal penetration) in all South African varieties of lantana that were inoculated (Retief 2010b).

Feeding by the leaf-sucking mirid, *F. intermedia*, induces *L. camara* (*s.l.*) to increase leaf toughness, and to double the density of trichomes on developing leaves in less than five weeks (Heshula 2009; Heshula *et al.* 2009), and this correlates with a substantial decrease in abundance of the biological control agent. Infested plants also emit 2.5 times as much beta-caryophyllene into the surrounding air (Heshula 2009), a kairomone known to attract an egg parasitoid of another heteropteran. The phenomenon of induced resistance is evidently a reality, and one of the factors hampering biocontrol of lantana.

Allelochemicals

Host specificity of phytophagous insects is usually determined by plant secondary metabolites, *i.e.* allelochemicals, that elicit or deter feeding and oviposition, and stimulate or inhibit development (Jaenike 1990). Most candidate agents for lantana that have been rejected were done so on the grounds of their unacceptable use of indige-

nous African *Lippia* spp. in quarantine (Heystek & Baars 2001, 2005; Baars 2002a; Phenye & Simelane 2005; Mabuda 2005; Williams 2002, 2004; Williams & Hill 2004; Williams & Duckett 2005). In cage tests, most candidates collected from New World *Lantana* taxa preferred to oviposit, and developed more successfully, on indigenous African *Lippia* spp., especially *Lippia rehmannii* and *Lippia* sp. B, than on indigenous African *Lantana* spp. Only two candidates (*C. pygmaea* and *P. griseipilis*) showed a closer affinity with an African congener (*Lantana rugosa*) of the source plant than with an African *Lippia* sp. (Williams 2004; F. Heystek & Y. Kisten-samy, unpubl.).

About 58 allelochemicals have been isolated from varieties of *L. camara* (*s.l.*) (Ghisalberti 2000), any one, or combination, of which could elicit or deter feeding or oviposition by phytophagous insects, and stimulate or prevent infection by fungi. *Lantana* varieties vary greatly in the concentration and type of their triterpenes (Hart *et al.* 1976). The Australian *Lantana* variety Townsville Prickly Orange, which is relatively non-toxic and non-invasive, contains relatively low concentrations of lantadene A and B and icterogenin (Hart *et al.* 1976; Kellerman *et al.* 2005), which may be part of the allelochemical *milieu* to which many natural enemies of New World *Lantana* taxa are adapted. Their acceptance of non-target *Lippia rehmannii* as a host plant, leading to the rejection of some candidate agents, may be due to their pre-adaptation to its main allelochemical, rehmamic acid, which is the same as lantadene A of *Lantana* (Hart *et al.* 1976; Everist 1981; van Wyk *et al.* 2002). Both plants also contain some icterogenin (Roets 1937; van Wyk *et al.* 2002).

Other candidate agents are rejected because of their apparent inability to breed sustainably on the target weed, *L. camara* (*s.l.*), which could be due to their inability to cope with the relatively high concentrations of lantadene A and B and other triterpenes, which are present in *Lantana* varieties that are toxic and invasive, such as Australian Common Pink-edged Red (Hart *et al.* 1976).

The genetically-coded ability to synthesize these allelochemicals may have been present in the ancestral stock that gave rise to the genera *Lippia* and *Lantana*, in Gondwana, before Africa and South America separated about 150 Mya. It complicates the acquisition of suitable agents for biological control of *L. camara* (*s.l.*) in Africa.

However, biological control has also benefited,

in that pre-adaptation of *H. laceratalis* and *Aristaea onychota* to similar allelochemicals in their indigenous, African host plants, which are in the genera *Lantana* and *Lippia* (Kroon 1999), is probably the reason they were able to colonize the introduced, Neotropical *L. camara* (*s.l.*). The former species is the most abundant phytophage on *lantana* in South Africa (Table 2) and Swaziland (Magagula 2010), whilst the potential abundance of the latter is curbed by extremely high levels of parasitism (Baars 2003).

Allopolyploidy

Different varieties of *L. camara* (*s.l.*) yield different quantities of allelochemicals, with different pentacyclic triterpenoids predominating in their spectra (Hart *et al.* 1976). Toxicity and invasiveness are greater in *lantana* varieties which have a greater concentration of the same allelochemicals (Hart *et al.* 1976). The *lantana* taxa vary from diploid to hexaploid (Stirton 1977; Sanders 2006) and the invasive taxa are mostly tetraploids (Spies 1984a). Invasive tetraploids are therefore likely to have a higher concentration of allelochemicals than non-invasive diploids. Most natural enemies probably co-evolved with and are best adapted to the diploid, wild *Lantana* spp. Surprisingly, in the West Indies, polyploid *Lantana* taxa are more abundant and widespread than diploid taxa (Day *et al.* 2003a). Consequently, many natural enemies may be equally well adapted to the autopolyploid forms of their host *Lantana* species, *i.e.* able to cope with a higher than normal concentration of the diploid's spectrum of allelochemicals.

However, the chromosomes of the weedy *lantanas*, and the high frequency of meiotic irregularities, indicate that they are allopolyploids, *i.e.* interspecific hybrids (Spies 1984a; Sanders 1987, 2006; J.J. Spies, pers. comm.). Allopolyploids probably have the genetically coded ability to synthesize the spectra of allelochemicals of both parental species. Few natural enemies are likely to be well adapted to coping with the broadened spectrum of defensive chemicals present in an allopolyploid. Accordingly, we hypothesize that the intractability of weedy *lantana* to biological control, *i.e.* the low overall effectiveness of *lantana* biological control agents, as seen in their generally low population densities (Table 2; Magagula 2010) and low, long-term impact on the target weed (Day *et al.* 2003a), is probably partly because weedy *lantana* comprises a suite of different allopolyploids,

which not only possess the capacity for hybrid growth and reproductive vigour, but also, individually and collectively, produce a far broader spectrum of defensive allelochemicals than most biological control agents are adapted to cope with.

Allopolyploidy, and the consequent diversity and potency of defensive chemicals, seems to account for both the hybrid vigour of lantana and its resistance to biological control agents. Resistance factors can have an additive impact on phytophagous insects (Chen 2008). The addition of more genetic material to the lantana complex, through the introduction and cultivation of even so-called 'sterile', ornamental varieties of *Lantana*, should therefore be opposed (Spies & du Plessis 1987). The 'sterile', yellow, groundcover lantana, which is called '*Lantana camara* cv. Sundancer' in Australia (Ellison 1995), and was marketed in South Africa as a '*Lantana montevidensis* hybrid', is in reality a hybrid between *L. (×)strigocamara* and *L. depressa* var. *depressa* (Sanders 1987, 2001, 2006). Sundancer cross-pollinates with *L. camara* (s.l.) (Neal 1999; Henderson 2009; A.J. Urban & L. Henderson, unpubl.), thus adding its resistance genes to the lantana gene pool and potentially making the weedy complex even more intractable to biological control. In view of this concern, Sundancer was banned in Australia, and was voluntarily withdrawn from the nursery trade in South Africa (J. Malan, pers. comm.).

Interspecific competition

The post-release population explosion of *O. camarae* on the coast of KZN coincided with a population crash of an established agent, *U. girardi* (Heystek 2006). As both are leaf miners, and both prefer the same lantana variety in the same area, it was hypothesized that the reduction in *U. girardi* populations was due to interspecific competition (Heystek 2006). Semi-field and field studies showed that there is some mutual interference between these agents, in that prior infestation of leaves by *U. girardi* makes them less attractive for oviposition by *O. camarae*, and prior infestation by *O. camarae* causes co-infested leaves to abscise earlier, reducing survival mainly of *U. girardi* (April 2009; April *et al.* 2009). However, these agents coexist in the field, and the impact on lantana appears to have become greater since the introduction of *O. camarae* (D.O. Simelane, pers. obs.).

ROLE OF BIOLOGICAL CONTROL IN MANAGEMENT OF LANTANA

Degree of control achieved

Lantana biological control agents such as *T. scrupulosa* and *O. scabripennis* occasionally completely defoliate whole stands of lantana. However, their impact, though striking, is only temporary, and the plants soon recover. The lack of a persistent, conspicuous, visual impact leads many observers to question whether adequate biological control of lantana is achievable (Johannsmeier 2001; Zalucki *et al.* 2007). According to the commonly accepted criterion that a problem is only 'under control' when it is being held static or diminishing, lantana is indeed 'out of control', because, overall, the infestation is becoming denser and spreading. The suite of biological control agents currently established is inadequate: it neither kills the lantana plants, nor stops the weed population increasing. However, the biological control agents do reduce the rate of growth and reproduction of lantana, and thus, as may be surmised (Harper 1977), its rate of increase in density and spread.

According to the criteria used in this volume (Klein 2011), the degree of control (*i.e.* reduction in weed-status) of lantana through biological control alone is somewhere between 'negligible' and 'substantial', because control of the weed remains entirely reliant upon the implementation of other control measures, although biological control does reduce the frequency and cost of those other control actions. Getting rid of lantana requires mechanical plus chemical treatment; biological control plays a subsidiary role, in that it reduces the frequency and cost of control actions (Urban 2010).

Economic benefits

When lantana infested approximately 2.2 million ha of grazing land in Australia in 2005–2006, the cost to the grazing sector was calculated to be approximately AU\$104.3 million *per annum* in terms of lost productivity and increased management expenses (AECgroup 2007). Lost productivity accounts for 74 % of the cost. In addition, land values were reduced, and about 1300 native species were adversely affected (Anthony 2008). The extent of the lantana infestation in South Africa is currently 0.56 million ha of landscape and riparian areas (Kotze *et al.* 2010). Assuming that

50 % of the infestation is on grazing land, and extrapolating from the Australian calculations, the lost productivity alone is costing stock farmers in South Africa approximately R67 million per annum.

In Australia, it was calculated that if a hypothetical lantana biological control research programme, funded at the rate of AU\$0.3 million/annum (about R2 million per annum), managed to achieve a 50 % reduction in the impact of the weed on grazing lands after 15 years, the benefit:cost ratio would be about 90:1 (AECgroup 2007).

In South Africa, the established suite of biological control agents is estimated to be reducing the rate of growth and reproduction of lantana by about 40 % (Cilliers 1987b; C.J. Cilliers, pers. comm.), which is reducing the rate of increase in density and spread, although not making the rate zero or negative. Benefit:cost analyses indicated that the return to South Africa on State investment in lantana biological control research is 8- to 34-fold, in terms of the reduction in rate of loss of pasturage (van Wilgen *et al.* 2004), and 50-fold for lantana and other invasive alien subtropical shrubs as a group, in terms of the reduction in rate of loss of ecosystem services (*i.e.* water resources, pasturage and biodiversity) (de Lange & van Wilgen 2010). The average degree of control achieved by lantana biological control agents on mainland areas is estimated to be about 26 % (Zalucki *et al.* 2007). Assuming, conservatively, that biological control of lantana is reducing the loss of pasturage and other ecosystem services by only 10 % overall, would put the value of lantana biological control in South Africa at at least R7 million per annum, which far exceeds current expenditure on lantana biological control research.

CONCLUSIONS AND FUTURE RESEARCH

Referring to the array of weedy, mainly hybrid lantana entities of horticultural origin as '*L. camara* (*s.l.*)', is supported as a convenient way to avoid confusion with the wild species, *L. camara* L. Recent morphological and genetic analysis indicates that it is justified to explore for promising natural enemies on all *camara*-like *Lantana* taxa, including *L. camara* (*s.l.*), between Florida and Uruguay. Further exploration may be worthwhile in the northwestern quadrant of South America, and, to fill the greatest need, especially in areas with a continental climate and a dry winter.

South African research into the biological control

of lantana from 1987 to 2010 covered 30 candidate agents, of which 15 were rejected as unsuitable, seven were shelved, seven were found suitable for release into Africa, and one is still being evaluated in quarantine. Of the six new agents released so far, five are showing signs of at least initial establishment, and two (*A. lantanae* and *O. camarae*) are improving suppression of *L. camara* (*s.l.*) in the humid, frost-free coastal zone. No significant non-target effects have been detected.

Lantana biological control agents are scarce overall in South Africa, especially in the inland areas, which are drier and colder. Agent proliferation is constrained by a combination of climatic incompatibility, acquired natural enemies and, probably, plant allelochemicals. It is hypothesized that plant allelochemicals play a key role in several phenomena: (i) the utilization of indigenous African *Lippia* spp., which makes many candidate lantana biological control agents unsuitable for release into Africa, is due to their containing allelochemicals similar to those of Neotropical *Lantana* spp; (ii) the colonization of *L. camara* (*s.l.*) by phytophages from indigenous African *Lantana* and *Lippia* spp. is due to their pre-adaptation to similar allelochemicals; (iii) the differential resistance of lantana varieties to biological control agents is partly due to their qualitatively and quantitatively different spectra of allelochemicals; (iv) the induction of resistance in lantana is due to phytophages and pathogens stimulating the plant to increase biosynthesis of allelochemicals conferring resistance; and (v) the intractability of lantana to biological control is because it comprises an array of allopolyploids, which provides the genetic capability not only for hybrid growth and reproductive vigour, but also, individually and collectively, to produce an exceptionally broad spectrum of defensive allelochemicals that confer a degree of resistance to most biological control agents.

In the case of lantana, biological control plays a subsidiary role, in support of essential, mechanical-plus-chemical control. Despite agent impact being limited, the socio-economic benefits that accrue definitely justify the development of additional lantana biological control agents.

The following short- to medium-term actions are proposed:

1. Expand the mass-rearing and release of *C. camarae* and *L. bethae*, and the harvesting and redistribution of *A. lantanae*; monitor their establishment and evaluate their impact.

2. Measure the maximal impact of all established biological control agents on lantana on the coast of KZN, and their limited impact in an inland area in MP.
3. Re-collect *O. ignifera* from Mexico or the southern U.S.A., for brief culturing in quarantine, confirmation of identity, mass-rearing and release.
4. Collect a high-altitude-adapted strain of *O. camarae*, and a shoot-tip boring strain of *C. lantana* from the central highlands of Mexico, to extend agent impact.
5. Re-collect *T. vulgata* from southeastern Brazil, and re-assess its suitability, using naturalistic, large-cage, fresh-air conditions.
6. Import *P. lantanae* isolate IMI 398849 from CABL, for further pathogenicity testing in quarantine, if the initial testing in the U.K. shows it to be potentially safe for release into Africa.
7. Re-import *L. columbicus columbicus* from Venezuela, or another root feeder, for host-specificity testing in quarantine, to supplement the action of *L. bethae*.
8. Supply additional triplicate specimens of *camara*-like *Lantana* taxa to Biosecurity Queensland, for morphological analysis by BRI, Texas, and genetic analysis by CSIRO, Australia.
9. Survey for promising natural enemies of *camara*-like *Lantana* taxa, including horticultural varieties of *L. camara* (*s.l.*), in the north-western quadrant of South America, especially in areas with a continental climate and a dry winter.

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