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Biology, oviposition preference and impact in quarantine of the petiole-galling weevil, *Coelocephalapion camarae* Kissinger, a promising candidate agent for biological control of *Lantana camara*

J-R. Baars [a,b,*], M.P. Hill [a,c], F. Heystek [a], S. Neser [a], A.J. Urban [a]

[a] *ARC-Plant Protection Research Institute, Weeds Research Division, Private Bag X134, Queenswood 0121, South Africa*
[b] *School of Biology and Environmental Science, University College Dublin, Limnology Unit, Belfield D4, Dublin, Ireland*
[c] *Rhodes University, Department of Zoology and Entomology, Grahamstown, South Africa*

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Abstract

The petiole-galling weevil, *Coelocephalapion camarae* Kissinger (Coleoptera: Brentidae), native to Mexico, was introduced into quarantine in South Africa to evaluate its potential to supplement the biological control programme against the invasive varieties of *Lantana camara* L. (Verbenaceae). The weevil occurs over a wide, native, geographic range, indicating its physiological potential to establish and persist throughout the range of climatic conditions under which the target weed grows in South Africa. The adults are highly selective in their choice of oviposition site, and only leaf-petioles with a width larger than 1.5 mm are accepted. Emerging larvae burrow into the vascular tissue and induce gall formation. Galling disrupts the transport of water and nutrients to and from the leaf, causing it to desiccate. During glasshouse studies the effect of galling on plant growth was tested on two different lantana varieties. The apionine both reduced lantana biomass accumulation (from 2 to 43% dry mass), and altered subsequent resource allocation away from the roots in both lantana varieties. Root growth increment loss over the duration of the trials on medium-density beetle-colonized plants (10 adult pairs) was between 109 and 144%, and increased from 109 to 117% in high-density beetle-colonized plants (20 adult pairs). These studies suggest that *C. camarae* could make a valuable contribution to the biocontrol programme against *L. camara*, and that studies on its host specificity are warranted.

Keywords: Coelocephalapion camarae; Coleoptera; Brentidae; Apioninae; Lantana camara; Verbenaceae; Pre-release studies; Gall formation; Impact assessment; South Africa

1. Introduction

The invasive alien plant, *Lantana camara* L. (Verbenaceae), has been the target of a biological control programme in South Africa since 1960 but still flourishes and requires supplementary control interventions (Cilliers and Neser, 1991; Baars and Neser, 1999; Baars, 2003; Baars and Heystek, 2003). Some additional candidate agents recently evaluated in quarantine proved insufficiently host-specific for release into Africa (Heystek and Baars, 2005; Mabuda, 2005; Phenye and Simelane, 2005; Williams and Duckett, 2005), whilst others that were suitable (Simelane, 2002; Baars et al., 2003; Den Breeÿen and Morris, 2003) have had geographically limited impacts, indicating a persisting need for new agents that promise sustained and widespread suppression of the target weed.

Some apionine weevils have proven to be effective weed biocontrol agents, notably *Trichapion lativentre* (Beguin-Billecocq) in the seed-pods of *Sesbania punicea* (Cav.) Benth. in South Africa, *Coelocephalapion pigrae* Kissinger in the inflorescences of *Mimosa pigra* L. in Australia, *Perapion antiquum* (Gyllenhal) in the stems of *Emex australis* Steinh. above 600 m in Hawaii, *Apion fuscirostre* (Fab.) in the seed-pods of *Cytisus scoparius* L. in western USA, and *Omphalapion hooker*

* Corresponding author. Present address: 3 Sunnyhill, Castlemartin lodge, Kilcullen, Co. Kildare, Ireland.
E-mail address: janrobert.baars@ucd.ie (J-R. Baars).

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Kirby in the seed-heads of *Tripleurospermum inodorum* (L.) Schultz Bip. in Canada (Julien and Griffiths, 1998). The first biocontrol agents released on *Lantana camara* in Hawaii in 1902 included two apionines, listed as *Apion* sp. A and *Apion* sp. B, from Mexico (Perkins and Swezey, 1924), but they did not establish (Gardner and Davis, 1982). Further surveys of phytophages on *Lantana* spp. in Mexico yielded *Coelocephalapion* sp. nr. *fusciventre* (Palmer and Pullen, 1995), but it was rare and not considered promising. Subsequent collections included an apionine that was described as *Coelocephalapion camarae* (Coleoptera: Brentidae) (Kissinger, 2000), and during its evaluation as a candidate biocontrol agent for *Lantana camara* in South Africa, it was found to be a leaf-petiole galler.

The success of endophagous insect agents on some other South African weeds (Hoffmann and Moran, 1999) supports the selection of endophagous candidate agents for *L. camara*, although some leaf miners, like *Calycomyza lantanae* (Frick) and *Octotoma scabripennis* Guérin-Méneville have not provided sufficient stress on lantana (Baars and Heystek, 2003). In particular, gall-inducing agents have been successful in some biocontrol programmes, particularly when the gall acts as a metabolic sink (Dennill, 1988; Harris and Shorthouse, 1996). In addition, the close association of gall inducers with their hosts implies a narrow host range (Forno et al., 1994; Harris and Shorthouse, 1996), reducing the risk of non-target effects.

In this paper, we describe the life history, gall characteristics and damage caused by the weevil, in an attempt to predict the contribution that *C. camarae* may make to biological control of *L. camara*.

2. Materials and methods

Coelocephalapion camarae was collected from a *Lantana* species, probably *L. camara* (S. Neser, personal communication) at Cárdenas (Tabasco Province, Mexico) during a survey in October 1997. This apionine weevil was cultured in the quarantine laboratories and glasshouses of the Plant Protection Research Institute (Pretoria, South Africa), where life history and impact studies were conducted. Laboratory cultures were maintained at 21–28 °C, 60–70% RH and a 13 h photoperiod. The glasshouse studies were subject to temperatures of 20–30 °C and a natural summer photoperiod of about 14 h.

Reference plants were made from cuttings from eight different *L. camara* varieties naturalised in South Africa. These varieties were selected to represent the range of morphological variation present in South Africa, notably of growth form, leaf characteristics, leaf-petiole size, shoot tip characteristics and flower colour (Table 1). All test plants were propagated under 50% shade net, with overhead irrigation, and grown in a standard growing medium of loam, coarse river sand and compost.

The results from trials described below were analysed using an ANOVA and Fisher's Protected LSD at the 5% level (Genstat 5, 1993), unless otherwise specified.

2.1. Native distribution and field status

A limited field survey was conducted in Mexico to determine the distribution patterns of *C. camarae*. Thirty-six sites were sampled along the gulf coast, from Merida (Yucatan Province) to Tampico (Veracruz Province) in October 1998. Sites were selected where *L. camara* plants were common, with at least 10 plants occurring in close proximity to each other. The habitats sampled included roadsides, stream banks, boundaries of farmlands and natural vegetation. At each site, at least 10 plants were sampled, and two to three sections of each plant were shaken above a beating tray to dislodge the weevils for collection. To quantify gall development, the available leaf-petiole

Table 1
Origin and key characteristic descriptions of the *L. camara* varieties from South Africa used during trials, selected as reference plants representing the major weed varieties growing as extensive field infestations

Lantana camara Variety	Origin: town/province	Grid reference	Distinguishing morphological characteristics	Flower colour[a]
009	Sycamore Mpumalanga	25°35′13.7″S 30°27′08.5″E	Spiny and hairy shoot tips; leaves hairy; main stem with few spines	Light-pink
012	Sycamore Mpumalanga	25°35′13.7″S 30°27′08.5″E	Shoot tip very spiny; leaves small and hairy; main stem very spiny	Light-pink
015	Kiepersol Mpumalanga	25°02′21.6″S 31°02′19.8″E	Shoot tip spiny; large broad dark hairy leaves; main stem spiny	White
017	Sabie east Mpumalanga	25°03′17.1″S 30°57′03.6″E	Shoot tip hairy, spiny and reddish in colour; leaves hairy and small; hairy main stem with few spines	Orange-reddish pink
018	Sabie Mpumalanga	25°07′04.9″S 30°45′39.2″E	Shoot tip spiny; leaves large, thick and tough; main stem spiny	Dark-pink
029	Hazyview Mpumalanga	25°08′10.6″S 30°00′09.0″E	Shoot tip spiny; large broad dark hairy leaves; main stem spiny	White-pink
150	La Mercy KwaZulu- Natal	29°38′45.9″S 31°07′39.5″E	Scrambling shrub; shoot tips hairy, spiny and reddish in colour; leaves small and hairy	Orange
163	Scottburgh KwaZulu- Natal	30°09′08.4″S 30°49′39.7″E	Spiny and hairy shoot tips; leaves hairy; main stem with few spines	Light-pink

[a] Colour of mature flowers.

galls of *C. camarae* were collected and their status of development was subsequently determined by dissection.

2.2. Rearing technique

The weevil culture in quarantine originated from the six adults imported in 1997. Insect cultures were typically initiated using a group of up to 100 adults, confined for 5–7 days, on a single *L. camara* plant in a gauze cage (90 × 45 × 45 cm). The weevils were then removed and mixed in equal proportions with weevils from other cultures to maintain a diverse genetic pool, before new cultures were initiated.

2.3. Life history

Observations were made on cultures of *C. camarae* maintained in quarantine over a two and a half year period. The number of larval instars and duration of the life stages were determined by dissecting infested leaves sequentially during trials. One hundred adults were exposed to *L. camara* (var. 163) for 2 d at a time. The same adults were exposed to a total of eight plants. Three to five infected leaves were dissected every 1–2 d, the life stages recorded, and the larval head-capsule widths measured.

To determine the pre-oviposition period, 10 newly emerged adults were exposed daily to 20 cm *L. camara* (var. 009) shoot-tip cuttings placed in saturated 'oasis' florist foam, isolated in a 3-l container. The cuttings were examined and leaves dissected daily to record the commencement of oviposition. The experiment was repeated with six groups of adults.

2.4. Oviposition and feeding preference

The oviposition and feeding behaviour of *C. camarae* was observed during both a field survey and laboratory trials. Petiole utilization for oviposition, was measured at a field site in Palma Sola (Veracruz Province, Mexico), where high levels of adult *C. camarae* and damage were observed. At this site, an uninhabited, rural landscape, *L. camara* plants were abundant and ranged from small seedlings to 1-m tall multi-stemmed shrubs. The top 30 cm of five branches was collected from each of three plants and petiole length (up to the first vein), maximum width, and leaf length and width were measured. Leaves with galls and characteristic larval damage were collected randomly from the remaining plants at the site and also measured.

During glasshouse studies, three *L. camara* (var. 163) plants were exposed to 10 pairs of adults for 5 d, in gauze cages. Each leaf was examined for eggs and feeding marks and the width and length of the leaf-petioles and width and length of the leaves were measured. The adults were then re-exposed to the same plants for a further 5 d, and the same measurements recorded, to examine oviposition behaviour when oviposition sites were limited. Results were subjected to linear regression analysis to determine the relationship between feeding and oviposition and the utilization of available plant resources.

2.5. Effect of galling on leaf longevity

The effect of leaf-petiole galls on leaf longevity was examined using five *L. camara* varieties, namely varieties 012, 015, 029, 150, and 163 (Table 1). Some 20–30 leaf-pairs were selected on three plants of each variety, and included leaves of different age, position on the stem and leaf-petiole size. The petioles were measured and tagged and one from each pair was covered with a paper straw to prevent oviposition by *C. camarae*. The straws were cut to the sizes of the leaf-petioles, from the stem to the first leaf-vein. Each plant was exposed to 15 pairs of adults in gauze cages. After 2 d, oviposition on the marked leaves was recorded, and the condition of the tagged leaves was recorded daily up to 2 weeks after the adult progeny emerged.

2.6. Effect of galling on plant growth and biomass accumulation

The impact of leaf-galling on the plant's growth rate was examined by exposing adults to two *L. camara* varieties, namely varieties 018 (leaves with thin petioles) and 017 (leaves with wide petioles) (Table 1). The trial plants were grown for five months and fertilized twice with 5 g of LAN. Twelve equally sized plants of variety 018 and nine of variety 017 were selected. Three control plants of each variety were sacrificed at the start of the trial (Control T_0) and the number of leaves and flowers and the wet and dry masses of the leaves, flowers, stems, and roots were recorded. The plant parts were dried at 80 °C for 48 h, and weighed on an electronic scale (Mettler PM400).

The numbers of leaves and flowers on the remaining plants were counted, and the plants were placed in gauze cages (93 × 45 × 45 cm) and kept in the glasshouse. Of these, a further three plants of each variety served as controls and were not exposed to the weevils (Control T_1), while three of each variety were exposed to 10 pairs of 3 week old beetles. Three plants of *L. camara* 018 were exposed to 20 pairs of adults. Adults were exposed to the plants for 5 d, after which the plants were removed from the cages. The plants were then maintained for 30 d and then cut down and the same parameters as above were measured. The numbers of leaf-petiole galls per plant was also recorded.

3. Results

3.1. Native distribution and field status

In addition to the original collection site at Cárdenas (Tabasco Province), adults and larvae of *C. camarae* were collected at six sites along the gulf coast of Mexico, during the 1998 survey (Fig. 1). When these records are combined with other locality records (Kissinger, 2000; A.J. Urban and S. Neser, personal observations), the distribution of *C. camarae* includes sites at altitudes between sea level and 1500 m and covers a wide geographic area (Fig. 1). The 1998 collections were confined to *L. camara*, but since the host plants

Fig. 1. The distribution of *Coelocephalapion camarae* in Mexico in relation to some large cities (■). This was determined from observations during surveys of *Lantana* species (△), and from locality records (Kissinger, 2000; A.J. Urban and S. Neser, personal observations) (○).

relating to previous collections are unknown (Kissinger, 2000), these may include other *Lantana* species.

At Palma Sola (Veracruz Province), *C. camarae* populations were high. At this site, 46 galled leaves were collected, of which 17% were parasitized (Fig. 2). Both larval and pupal hymenopteran parasitoids were observed, but were not reared for identification. Additional mortality was observed in some 20% of the galls, where the galls either aborted or the developing larvae or pupae had become squashed by excessive callus tissue (Fig. 2). Over 31% of the larvae were in their final instar and appeared healthy.

3.2. Life history

Eggs of *C. camarae* were usually inserted into the leaf-petiole, but also into the inflorescence-peduncle at the base of the receptacle. In the leaf-petioles the female chewed out a cavity in the strengthened parenchyma tissue and cambium layer, leaving the vascular tissue intact. The egg was deposited and secured in position near the vascular tissue, with a pale yellow secretion. The entrance of the cavity was then plugged with a thin layer of faecal deposit, which sealed the cavity. The female finally deposited a secretion onto the surface of the petiole, some 2 mm (mean ± SE: 1.86 ± 0.01 mm; $n = 94$) from the egg towards the stem, which served as an oviposition marker. The faecal plug and marker were clearly visible as two dots on the undersurface of the leaf-petiole (Fig. 3b). Eggs were deposited from near the stem up to the first leaf-vein. Petioles of all ages were utilized for oviposition. Eggs laid in the inflorescence-peduncles were inserted in a similar manner, but no oviposition marker was deposited. The eggs were pale white and ellipsoidal (Fig. 3a), approximately 0.5 mm in length, and took 6 d to hatch (Table 2).

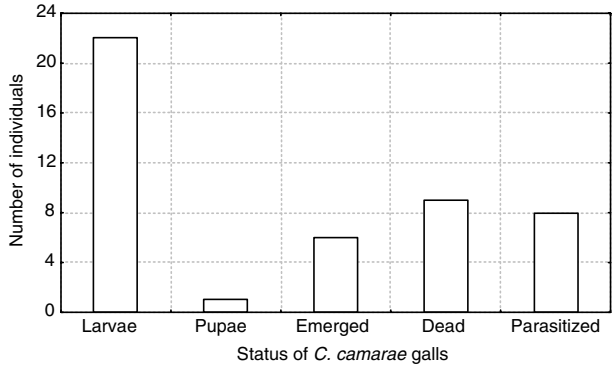

Fig. 2. The status of leaf-petiole galls of *Coelocephalapion camarae* collected in the field at Palma Sola (Veracruz Province, Mexico) (Total number of galls = 46).

The hatching first instar larva fed on the cambium and parenchyma tissue, tunnelling usually less than 3 mm towards the stem. The larva then fed on the vascular tissue, which stimulated the plant to produce proliferated tissue and initiate the galls. The larvae remained relatively sedentary and fed predominantly on the vascular and proliferated tissue. At the galling site most of the leaf-petiole tissue was damaged (in excess of 90%, depending on the size of the leaf-petiole), preventing the transport of solutes to and from the leaf, occasionally causing the leaf to desiccate (Fig. 3d). The gall continued to expand until the larva pupated. Pupation occurred inside a capsule, constructed from plant material and faecal deposits, within the gall. The gall was relatively small, not exceeding twice the width of the undamaged petiole and was not lignified. The larva was small, white with a light brown head-capsule, and had a C-shaped body (Fig. 3c). The larva passed through three instars and development from egg to adult took about 35 d (Table 2).

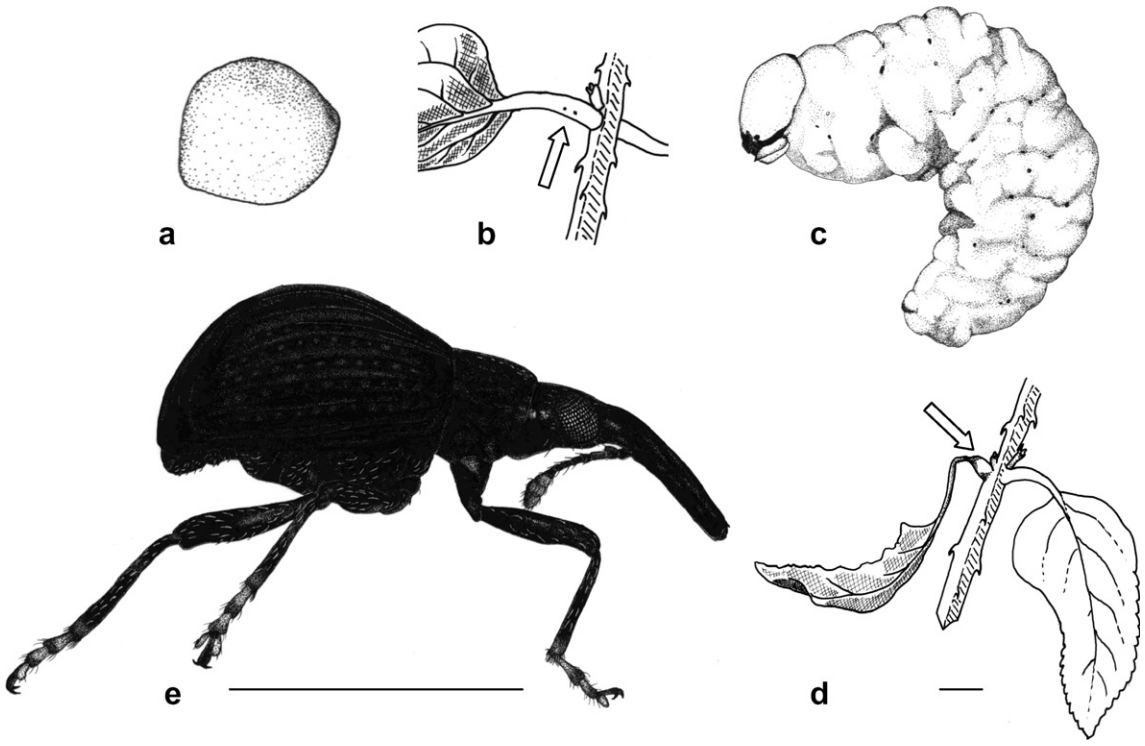

Fig. 3. Life stages and characteristics of *Coelocephalapion camarae*. (a) Egg; (b) egg deposited in a leaf-petiole with the oviposition marker; (c) final larval instar (third); (d) leaf-petiole gall induced by the larva, causing the leaf to desiccate (scale bar 10 mm); (e) female beetle (scale bar 2.0 mm).

Table 2
Details of the life stages of *Coelocephalapion camarae*

Life stage	Duration	n[a]	Measurements (mm)[b]	n[a]
Egg	6 days	35	0.46 ± 0.01 (length)	46
			0.35 ± 0.01 (width)	46
1st instar	5–6 days	32	0.23 ± 0.002[c]	50
2nd instar	5–7 days	26	0.28 ± 0.001[c]	50
3rd instar	10–12 days	31	0.38 ± 0.001[c]	50
Pupa	6–7 days	35		
Adult	10 d pre-oviposition	30	♀ 0.73 ± 0.01[d]	36
	4–6 months		♂ 0.63 ± 0.01[d]	36

[a] n = Number of individuals on which observations were made.
[b] Means ± standard error.
[c] Head capsule width of larvae.
[d] Length of the rostrum; as a sexually dimorphic character.

The emerging adult remained in the gall for a day, before chewing through an epidermal 'window' prepared by the larva and invisible from the outside. The adult was small, mostly black, and highly active (Fig. 3e). There was no distinct external morphological difference between the male and female, although the female generally had wider abdomen and longer rostrum (Table 2). Adults often occurred in pairs, in close proximity and positioned almost at right angles to one another, on the under-surface of the leaf. The male appeared to guard the female in this position. Mating occurred throughout the adult lifespan. Adults fed on the lower layers of the leaves, leaving the upper epidermal layers intact, and feeding damage resembled small 'shot-holes'. The adults also occurred on the flowers and occasionally fed on the corolla. The pre-oviposition period was about 10 d (mean ± SE: 10.0 ± 0.2 d; $n = 6$ groups of 10 adults), after which eggs were laid at a rate of approximately one per day. The adults were long-lived, with those in laboratory cultures surviving for at least 4–6 months. With the onset of winter, adults kept in the quarantine glasshouses aggregated at the base of plants, in dry curled-up leaves and in sheltered crevices. During this period, feeding and oviposition were markedly reduced (see Table 3).

3.3. Resource preference

The growth of *L. camara* plant parts is proportional, typically resulting in strong correlations between leaf-petiole width and leaf length ($r^2 = 0.87$, $n = 286$) and leaf-petiole width and length ($r^2 = 0.75$, $n = 317$), as well as between leaf length and leaf width ($r^2 = 0.92$, $n = 254$) and leaf length and leaf-petiole length ($r^2 = 0.79$, $n = 286$). The feeding of adults was considered random during the trials as the position of the scars were not correlated with leaf size ($r^2 = 0.08$, $n = 286$) and thus leaf-petiole length and width, and position on the branch ($r^2 = 0.18$, $n = 211$).

In the field *C. camarae* adult oviposition was restricted to leaf-petioles ⩾1.5 mm in width, which occurred on leaves ⩾55.2 mm in length (Fig. 4a). In the laboratory the pattern of feeding and oviposition was not significantly different between plants ($P > 0.05$) and the results were pooled for analysis. The pattern of oviposition in the laboratory was similar to that observed in the field, and egg-laying was limited to leaf-petioles ⩾1.5 mm in width (range: 1.5–3.0 mm), which occurred on leaves ⩾3.27 cm in length (range: 3.27–9.80 cm) (Fig. 4b). Since plant growth is proportional, these

Table 3
Intensity of leaf-petiole galling by *Coelocephalapion camarae* during impact studies involving two South African *L. camara* varieties

Lantana camara variety	Experimental treatment[a]	No. leaves[b]	No. galls[b,c]	Percent leaves galled
018	Control T_0	150.0 ± 16.5	0.0 (−)	0
	Control T_1	167.0 ± 9.5	0.0 (−)	0
	10 adult pairs	181.0 ± 9.1	33.3 ± 4.3	18.4
	20 adult pairs	125.7 ± 17.6	55.3 ± 4.2	44.0
017	Control T_0	151.3 ± 30.2	0.0 (−)	0
	Control T_1	205.0 ± 10.2	0.0 (−)	0
	10 adult pairs	208.7 ± 35.7	29.7 ± 1.3	14.2

[a] Plants sacrificed as controls: at the start of the trial (T_0), and at the conclusion of the trial (T_1).
[b] Means ± standard error.
[c] Number of galls recorded 35 days after adult exposure; (−) no value applicable.

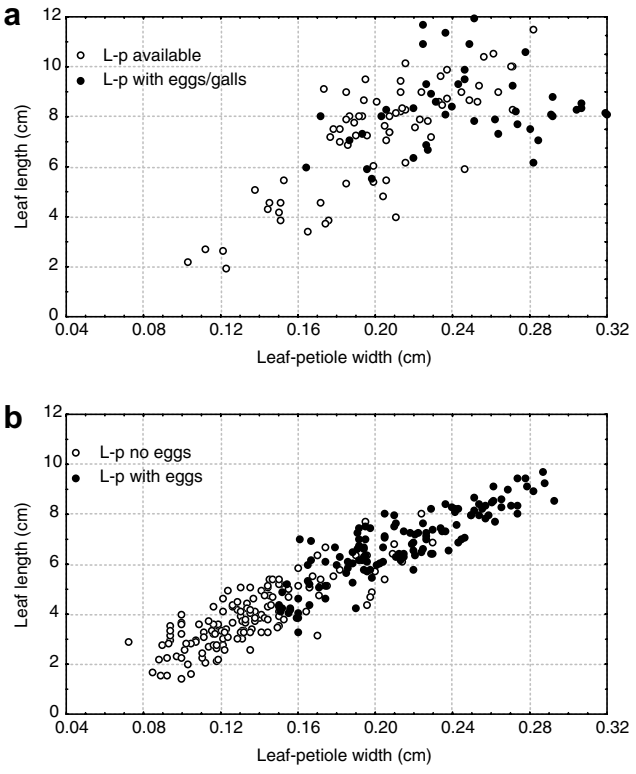

Fig. 4. The leaf-petioles (L-p) utilized by *Coelocephalapion camarae* amongst the leaf-petioles on (a) field *L. camara* plants at Palma Sola, Mexico; (b) a South African variety of *L. camara* (var. 163) exposed to the weevils in quarantine.

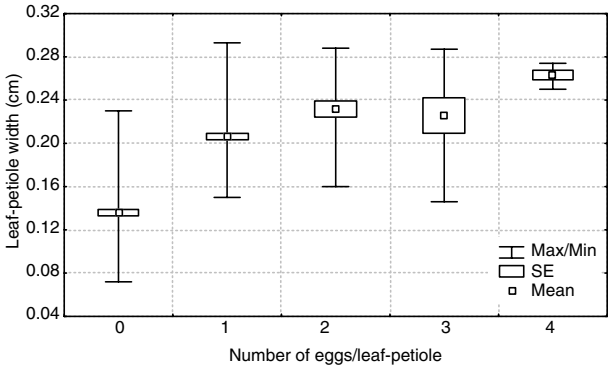

Fig. 5. The mean, standard error and width of leaf-petioles that contained 0–4 eggs, deposited by *Coelocephalapion camarae* adults that were exposed to a limited number of oviposition sites.

measurements typically apply to a minimum leaf-petiole length of 6.5 mm.

When adults were re-exposed to previously exposed plants, the patterns of resource utilization remained the same despite the shortage of oviposition sites. Leaf-petioles < 1.5 mm in width were not utilized as oviposition sites, while the remaining petioles were over-utilized with up to four eggs per petiole (Fig. 5). The intensity of oviposition was not correlated to petiole width ($r = ^2 0.20$, $n = 320$ leaves).

3.4. Effect of galling on leaf longevity

There were no significant differences in the longevity of galled leaves between the six *L. camara* varieties that were exposed ($P > 0.05$), and the results were poled for further analysis. Although a relatively low proportion of the galled leaves (37%) became desiccated during the experiment, none of the opposite leaves presented as the controls of the pairs became desiccated. Leaves took 11–31 d to desiccate ($n = 47$), and there was no significant correlation between leaf-petiole width and time taken for leaves to desiccate (Fig. 6). This indicates that the variation in larval damage to the vascular tissue of the leaf-petioles is not influenced by petiole width, plant variety or age of the leaf.

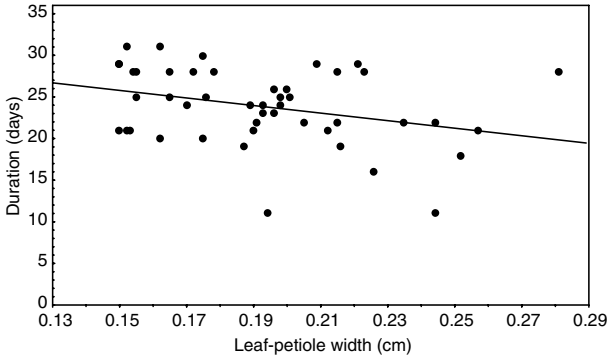

Fig. 6. The time taken for leaves to desiccate, on five South African *L. camara* varieties containing leaf-petiole galls of *Coelocephalapion camarae* ($r^2 = 0.10$, $n = 47$). There were no significant differences between varieties in the rate of leaf desiccation ($P > 0.05$).

3.5. Effect of galling on plant growth and biomass accumulation

The variation in biomass within the leaves, stems, roots, and flowers was low, indicating that the time zero control groups (Control T_0) for both lantana varieties were reliable in representing the state of the plants at the initiation of the experiments (Fig. 7). The two varieties used, despite being exposed to exactly the same planting and growing conditions, were different in size and the proportions of plant parts (Fig. 7). During the course of the trial, all of the plant material in the control groups (Control T_1) increased significantly in dry mass (Fig. 7).

In the case of *L. camara* variety 018, compared with the dry mass of the time zero control plants, the beetle-free plants grew 133% overall during the test period (Fig. 7a); the growth of leaves, stems, roots, and flowers being 128, 174, 106, and 184%. On this lantana variety, the medium- and high-density populations of *C. camarae* caused a total growth *increment* loss of 29 and 43%, respectively. These populations of the apionine caused a gain of 18% and loss of 26% in leaf growth, a loss of 2 and 5% in stem growth, a loss of 109 and 117% in root growth, and a loss of 19% and gain of 122% in flower growth.

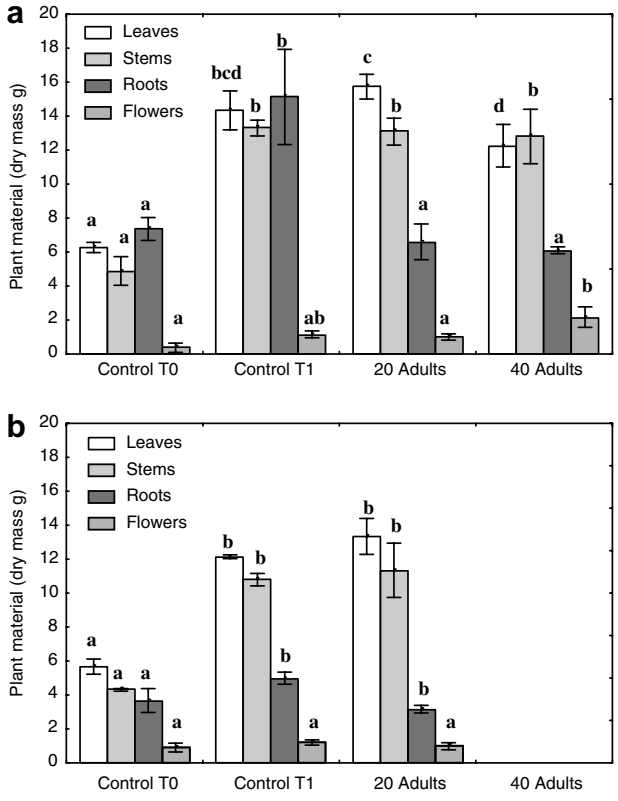

Fig. 7. The impact of leaf-petiole galls of *Coelocephalapion camarae* at medium- and high- density populations on tissues of two South African *L. camara* varieties, 018 (a) and 017 (b). The dry mass of plant material is grouped into leaves, stems, roots (material below where the first root arises from the stem) and flowers (including flower-stalks and seeds) for analysis. Control groups include the plants sacrificed at the beginning of trials (Control T_0) and at the conclusion of trials (Control T_1). A high-density population trial (40 adults) was not conducted on 017. Bars with the same letter are not significantly different (ANOVA, $P < 0.05$) within each plant material grouping.

In the case of *L. camara* variety 017, compared with the dry mass of the time zero control plants, the beetle-free plants grew 98% overall during the test period (Fig. 7b); the growth of leaves, stems, roots, and flowers being 112, 149, 32, and 36%. On this lantana variety, the (medium-density) population of *C. camarae* caused a total growth *increment* loss of only 2%. Leaf and stem growth of the beetle-colonized plants were 20 and 8% more than the controls, whilst root and flower growth *increments* were reduced by 144 and 80%, respectively.

The most consistent impact of *C. camarae* on *L. camara*, therefore, was to markedly stunt the growth of the roots. The apionine both reduced lantana biomass accumulation, and altered subsequent resource allocation away from the roots.

4. Discussion

Present distribution records of *C. camarae* indicate that it occurs over a wide geographic area in Mexico (Fig. 1), from sea level to 1500 m. The variations in climatic conditions over its native distribution range suggest that *C. camarae* may be pre-adapted to cope with the range of climatic conditions that occur over the distribution of *L. camara* in South Africa. However, the laboratory cultures of *C. camarae* used during this study originated from six individuals collected at a single locality. The laboratory population might therefore not be representative of the field population, and may need to be supplemented with individuals collected over a wide geographic range (Sands and Harley, 1981; Wapshere, 1985; Hopper et al., 1993). This has been considered necessary to not only increase the distribution of established agents on *L. camara* in South Africa (Neser and Cilliers, 1990), but also to improve the compatibility of the agents with the naturalized varieties of *L. camara* (Neser and Cilliers, 1990). If new genetic material of *C. camarae* is to be sourced, due consideration will have to be given to host range implications.

However, evidence of variation in behaviour and host range between biotypes of the cochineal bug, *Dactylopius opuntiae* (Cockerell), (Hoffmann et al., 1999) raises concerns that such differences may exist between populations of *C. camarae* that originate from geographically distinct areas within its native range. Furthermore, the highly successful apionine weevil, *Trichapion lativentre* (Béguin-Billecocq) has established throughout the range of its target host, *Sesbania punicea* (Cav.) Benth. (Papilionaceae), in South Africa, despite the inadvertent introduction of a very small founder population (Hoffmann and Moran, 1999). Due to a lack of evidence, the importance of adaptation following introduction and the procedures to improve adaptability through genetic diversity are still unclear (Hopper et al., 1993). In addition, the deliberate combining of previously genetically isolated populations may result in an ill-adapted population, and attempts at matching popula-

tions from the country of origin to climate areas in the introduced range separately may be more effective. The re-importation of a larger collection of adults should therefore be considered from the original collection site, or additional introductions from different areas should not be considered unless the releases fail to establish in South Africa.

The larvae of *C. camarae* inflict most of the damage and reduce the transport of solutes to and from leaves, by disrupting the vascular tissue in the leaf-petioles. This damage seems to stimulate the plants to compensate by altering the allocation of resources. The most noticeable short-term effect, at low galling densities, is a reduction in root biomass accumulation of 109, 117, and 144% relative to healthy plants (Fig. 7a and b). Plants in response compensate through a flush of new leaves, which is prevented at higher galling densities. The use of realistic population levels during damage assessments in cage experiments is essential for extrapolating the results to field conditions (Briese, 1996). Since it is difficult to predict the size of field populations that will develop after release, low population densities provide an indication of the minimum potential impact. The effect of *C. camarae* on *L. camara* is density related, but even low densities of galling are expected to augment the somewhat low levels of stress induced by most of the previously established biocontrol agents, which are predominantly leaf feeders (Baars, 2003; Baars and Heystek, 2003).

In the drier areas within the range of *L. camara* in South Africa, populations of many biocontrol agents tend to only recover from the high levels of winter mortality by mid summer (Cilliers, 1987; Baars, 2003; Baars and Heystek, 2003). As a result, *L. camara* populations are able to recover early in the new season, and compensate for cumulative agent damage from the previous growing season. The changes in the activity of adult *C. camarae* in glasshouses with the onset of winter conditions, combined with its longevity suggested that field populations may well diapause to survive the dry periods in South Africa as is typical in Mexico. *Coelocephalapion camarae* populations could therefore be expected to recover early in the growing season and sustain feeding pressure on *L. camara*.

The ability of biocontrol agents to assess and avoid oviposition sites used by conspecifics reduces the possibility of intraspecific competition between immatures for a limited resource (Heard, 1995). The use of oviposition markers allows *C. camarae* to effectively utilize the available leaves, thereby maximizing offspring survival and enhancing its potential as a biocontrol agent. The rejection of leaf-petioles below a threshold width has positive implications for host-specificity, since certain closely related non-target plant species may thereby be immune to oviposition by *C. camarae*. Although due consideration should be given to the utilization of the flower stalks of non-target species.

Coelocephalapion camarae is not the first apionine weevil to be considered for release against *L. camara*. Two *Apion* species were released against *L. camara* in Hawaii (Perkins and Swezey, 1924), but both failed to become established (Julien and Griffiths, 1998). Another species, *Coelocephalapion aduncirostre* (Gerstaecker), was recorded on *L. camara* during surveys in Mexico (Palmer and Pullen, 1995), but host records suggest a casual association because it has been reared from *Aeschynomene villosa* Poir. and *A. americana* L. (Fabaceae) (Kissinger, 1988). Two *Coelocephalapion* species were evaluated and released against *Mimosa pigra* L. in Australia (Forno et al., 1994; Heard and Forno, 1996), but their impact is as yet to be reliably quantified (Steinbauer et al., 2000).

The effectiveness of gall-inducing agents in biocontrol programmes (Harris and Shorthouse, 1996), and the potential of *C. camarae* as suggested by the results reported here, should encourage further investigations into similar endophagous species, as noted by Palmer and Pullen (1995). Furthermore, since the long-lived adults have the potential to diapause, *C. camarae* may be able to persist in the drier areas of South Africa, survive winter defoliation and sustain impact levels from the start of the growing season. *Coelocephalapion camarae* is a potentially effective biocontrol agent that, pending host-specificity test results be considered for release in South Africa and other countries where *L. camara* is problematic.

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References

Baars, J-R., 2003. Geographic range, impact, and parasitism of lepidopteran species associated with the invasive weed *Lantana camara* in South Africa. Biol. Control 28, 293–301.

Baars, J-R., Neser, S., 1999. Past and present initiatives on the biological control of *Lantana camara* (Verbenaceae) in South Africa. In: Olckers, T., Hill, M.P., (Eds.). Biological Control of Weeds in South Africa (1990–1998). Afr. Entomol. Mem. 1, 21–33.

Baars, J-R., Heystek, F., 2003. Geographic range and impact of five biocontrol agents established on *Lantana camara* in South Africa. Biocontrol 48, 742–759.

Baars, J-R., Urban, A.J., Hill, M., 2003. Biology, host range, and risk assessment supporting release in Africa of *Falconia intermedia* (Heteroptera: Miridae), a new biocontrol agent for *Lantana camara*. Biol. Control 28, 282–292.

Briese, D.T., 1996. Potential impact of the stem-boring weevil *Lixus cardui* on the growth and reproductive capacity of *Onopordum* thistles. Biocontrol Sci. Techn. 6, 251–261.

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

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

Den Breeÿen, A., Morris, M.J., 2003. Pathogenicity and host specificity of *Mycovellosiella lantanae* var. *lantanae*, a potential biocontrol agent for *Lantana camara* in South Africa. Biocontrol Sci. Techn. 13, 313–322.

Dennill, G.B., 1988. Why a gall former can be a good biocontrol agent—the gall wasp *Trichilogaster acaciaelongifoliae* and the weed *Acacia longifolia*. Ecol. Entomol. 13, 1–9.

Forno, W., Heard, T., Day, M.D., 1994. Host specificity and aspects of the biology of *Coelocephalapion aculeatum* (Coleoptera: Apionidae), a potential biological control agent of *Mimosa pigra* (Mimosaceae). Environ. Entomol. 23, 147–153.

Gardner, D.E., Davis, C.J., 1982. The prospects for biological control of nonnative plants in Hawaiian national parks. Cooperative Parks Studies Unit (Dept. Botany)/Univ. Hawaii. Technical Report 45. pp. 58.

Harris, P., Shorthouse, J.D., 1996. Effectiveness of gall inducers in weed biological control. Can. Entomol. 128, 1021–1055.

Heard, T., 1995. Oviposition and feeding preference of a flower-feeding weevil, *Coelocephalapion aculeatum*, in relation to conspecific damage to its host-plant. Entomol. Exp. Appl. 76, 203–209.

Heard, T.A., Forno, W., 1996. Host selection and host range of the flower-feeding weevil, *Coelocephalapion pigrae*, a potential biological control agent of *Mimosa pigra*. Biol. Control 6, 83–95.

Heystek, F., Baars, J-R., 2005. Biology and host range of *Aconophora compressa*, a candidate considered as a biocontrol agent of *Lantana camara* in Africa. Biocontrol 50, 359–373.

Hoffmann, J.H., Moran, V.C., 1999. A review of the agents and factors that have contributed to the successful biological control of *Sesbania punicea* (Cav.) Benth. (Papilionaceae) in South Africa. In: Olckers, T., Hill, M.P., (Eds.). Biological Control of Weeds in South Africa (1990–1998). Afr. Entomol. Mem. 1, 81–88.

Hoffmann, J.H., Moran, V.C., Zimmermann, H.G., 1999. Integrated management of *Opuntia stricta* (Haworth) Haworth (Cactaceae) in South Africa: an enhanced role for two, renowned, insect agents. In: Olckers, T., Hill, M.P., (Eds.). Biological Control of Weeds in South Africa (1990–1998). Afr. Entomol. Mem. 1, 15–20.

Hopper, K.R., Roush, R.T., Powell, W., 1993. Management of genetics of biological-control introductions. Annu. Rev. Entomol. 38, 27–51.

Julien, M.H., Griffiths, M.W., 1998. Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds, fourth ed. CABI Publishing, UK.

Kissinger, D.G., 1988. New host and distribution records for Apionidae from North and Central America (Coleoptera). Coleop. Bull. 42, 302–304.

Kissinger, D.G., 2000. A new species of *Coelocephalapion* Wagner (Brentidae) from Mexico with host *Lantana camara* L. (Verbenaceae). Coleop. Bull. 54, 365–369.

Mabuda, K., 2005. *Eutreta xanthochaeta* (Diptera: Tephritidae) is unsuitable for biocontrol of *Lantana camara* in Africa. Biocontrol Sci. Techn. 15 (6), 635–639.

Neser, S., Cilliers, C.J., 1990. Work towards biological control of *Lantana camara*: perspectives. In: Delfosse, E.S., (Ed.). Proceedings of the VII International Symposium on Biological Control of Weeds. 6–11 March 1988, Rome, Italy. Istituto Sperimentale per la Pathologia Vegetale, Ministero dell'Agricoltura e delle Foreste. pp. 363–369.

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

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

Phenye, M.S., Simelane, D.O., 2005. Arid-adapted Mexican leafhopper, *Barela parvisaccata* (Hemiptera: Cicadellidae), unsuitable for biocontrol of *Lantana camara* (Verbenaceae) in South Africa. Biocontrol Sci. Techn. 15 (6), 615–621.

Sands, D.P.A., Harley, K.L.S., 1981. Importance of geographic variation in agents selected for biological control of weeds. In: Delfosse, E.S., (Ed.). Proceedings of the V International Symposium on the Biological Control of Weeds, 22–27 July 1980, Brisbane, Australia. CSIRO, Melbourne, pp. 81–89.

Simelane, D.O., 2002. Biology and host range of *Ophiomyia camarae*, a biological control agent for *Lantana camara* in South Africa. Biocontrol 47, 575–585.

Steinbauer, M.J., Edwards, P.B., Hoskins, M., Schatz, T., Forno, W., 2000. Seasonal abundance of insect biocontrol agents of *Mimosa pigra* in the Northern Territory. Aust. J. Entomol. 39, 328–335.

Wapshere, A.J., 1985. Effectiveness of biological control agents for weeds: present quandries. Agric. Ecosyst. Environ. 13, 261–280.

Williams, H., Duckett, C., 2005. The trimorphic flea-beetle, *Alagoasa extreme*, not suitable for biocontrol of *Lantana camara* in Africa. Biocontrol 50 (4), 657–683.