Interaction between the root-feeding beetle, *Longitarsus bethae* (Coleoptera: Chrysomelidae) and the root-knot nematode, *Meloidogyne javanica* (Nematoda: Heteroderidae): Implications for the biological control of *Lantana camara* L. (Verbenaceae) in South Africa

A thesis submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE

At

Rhodes University

By

Jufter Musedeli

September 2018

Abstract

Plants often are simultaneously attacked by several herbivores that can affect each other's performance, and their interaction may affect their host plant fitness. The current study was conducted to determine the interaction between the root-feeding beetle, *Longitarsus bethae* Savini & Escalona (Coleoptera: Chrysomelidae) and a root-knot nematode, *Meloidogyne javanica* (Treub) Chitwood (Tylenchida: Heteroderidae), with implications for the biological control of *Lantana camara* L. (Verbenaceae) in South Africa. The studies were conducted under quarantine conditions at the Agricultural Research Council-PHP, Roodeplaat, Pretoria, South Africa. Specifically, the study determined; (i) whether root damage by the flea beetle enhanced infection by *M. javanica*, (ii) whether *L. camara* roots infected with the nematode enhanced the performance of the beetle, (iii) whether single or combined effect of the two organisms (i.e. *L. bethae* and *M. javanica*) had an overall effect on the growth and biomass of their shared host, *L. camara*, and (iv) the susceptibility of 10 *L. camara* varieties that are commonly found in South Africa to *M. javanica*.

The study found that galling on the roots of *L. camara* by the nematode occurs at the highest inoculation of 300 eggs of *L. bethae* per plant, and no galling occurred at inoculation of 200 eggs per plant and below. The findings also showed that *L. bethae* performed better on *M. javanica*-infected than on healthy *L. camara* roots, and that more *L. bethae* adult progeny with slightly bigger body size emerged from *M. javanica*-infected, than from healthy plants. Fresh weight (galls) of plant roots from treatments where both species (i.e., *L. bethae* and *M. javanica*) were combined was significantly higher than that from plants infected with the nematode only, suggesting that the combination of both species induces more galling than the nematode does alone. The above-ground dry biomass was significantly lower both in combined and *M. javanica* only treatments, than in *L. bethae* only treatment. The study also found that selected *L. camara* varieties were infected with *M. javanica*, albeit at varying degrees of infection. Among the 10 *L. camara* varieties, Orange Red OR 015 was the most susceptible. Other susceptible varieties included Light Pink 009 LP, Total Pink 021 TP and Dark Pink 018 DP, and these, together with variety Orange Red OR 015, constituted 40% of the *L. camara* varieties evaluated in the current study. Fifty percent of the varieties displayed slight to moderate susceptibility to *M. javanica*, while 10% displayed lack of susceptibility.

The study concluded that the symbiotic relationship between *L. bethae* and *M. javanica* was mutual, resulting in increase in the fitness of the beetle. The combined herbivory by *L.*

bethae and *M. javanica* was also found to be additive on one of the most common varieties of *L. camara* in South Africa, and therefore co-infestation by both species might enhance the biological control of this weed in South Africa. The study further concluded that the suitability of some invasive *L. camara* cultivars such as Light Pink 009 LP and Orange Red 015 OR for *M. javanica*, might also contribute towards biological control of this weed in South Africa, particularly in areas where the two herbivores species co-exist.

Keywords: Interactions; additive effect; biocontrol; *Lantana camara*; *Longitarsus bethae*; *Meloidogyne javanica.*

Table of contents

List of figures

List of tables

Acknowledgements

I would like to extend my sincere gratitude to:

- My mentor, academic father and supervisor, Dr D.O. Simelane (ARC-PHP weeds research) for his thorough guidance, constructive suggestions, criticism and motivations throughout the course of the study, it was an excellent opportunity to work under his supervision. I could not have asked for a better supervisor.
- Dr Mariette Marais (ARC-PHP Biosystematics) for her patience and fruitful efforts on giving me guidance concerning my nematode cultures and experiments to give affirmative outputs.
- Prof. Martin Hill (Rhodes University) for constructive inputs and advice on previous versions of the manuscript.
- Khethani Mawela (ARC-PHP researcher) for helping with data analysis (statistics) throughout the study patiently.
- Dr R. S. Nofemela, Hildegard Klein and Lulama Madire (ARC-PHP researchers) for wise and constructive advice that built potential and confidence in me.
- Tshililo Mphephu and Ludzula Mukwevho (Former ARC-PHP Junior Researchers) for helping me with time management and making sure that I do not relax during data collection and write-up phase.
- Staff of the Agricultural Research Council-Plant Health and Protection (ARC-PHP) for their contributions to the study, in particular Ayanda Nongogo, Khotso Malatji, Mukonazwothe Netshiluvhi and Kedibone Mofokeng for providing me with motivation when things did not seem to go well and technical assistance throughout data collection period.
- Anonymous reviewers who critiqued my dissertation with patience and spotted all the errors, Asante sana!
- My parents (Frederick and Julia Musedeli) for always bringing me hope and joy in times of trouble and my brothers (Cedrick, Theophelus, Innocent) for always believing in me in every journey that I embark on, you guys are the best in my life.
- ARC-PHP for allowing me to be hosted as part of the Professional Development Programme (PDP) for two years with ease.
- National Research Foundation (NRF) for funding my study.

- Finally, I thank the almighty God, who gave me strength when I needed it most to showcase my abilities, for protecting my life and for shining the light when days seemed to be dark. If it were not for grace and the love of God, none of this would have been achieved.

Declaration

I, Jufter Nndwamato Musedeli, declare that this thesis is my original work and has not been submitted for any degree at any other university or institution. The thesis does not contain other persons' writing unless specifically acknowledged and referenced accordingly.

Signed (Jufter Musedeli)…………………………… Date: ……………………………..

Signed (Prof Martin Hill): …………………………. Date: ……………………………..

Signed (Dr David Simelane): ……………………….. Date: ……………………………..

Signed (Dr Mariette Marais): ……………………….. Date: ……………………………..

CHAPTER ONE

GENERAL INTRODUCTION

1.1 Background to the study

Lantana camara L. (Verbenaceae), commonly known as lantana, is a highly invasive weed in South Africa. A biological control programme against this invader is on-going at Agricultural Research Council-Plant Health and Protection (ARC-PHP), with over a dozen biological control agents fully established on the weed in South Africa (Baars & Neser 1999; Day & Neser 2000; Baars & Heytek 2003). The root-feeding beetle *Longitarsus bethae* Savini & Escalona (Coleoptera: Chrysomelidae) is among the three agents released against lantana during the last decade, and has established at a few sites in Mpumalanga and KwaZulu-Natal provinces (D. Simelane ARC-PHP pers. com.). With the exception of the larvae of *L. bethae*, all other lantana biological control agents are aboveground herbivores. Lantana roots infested with *L. bethae* larvae often are associated with a root-knot nematode, *Meloidogyne javanica* (Treub) Chitwood (Tylenchida: Heteroderidae) (Simelane 2005), a parasite of various plant species in South Africa (Marais et al. 2017, Visagie et al. 2018). Interactions between natural enemies and how they impact their invasive hosts have received little research attention (Denoth et al. 2002). Therefore, this study investigated the nature of the relationship between *L. bethae* and *M. javanica*, and determine if the individual or combined effects of the insect and the nematode were beneficial to the biological control of lantana. The study further determined the potential contribution of *M. javanica* to *L. camara* biocontrol in South Africa by evaluating the nematode susceptibility of the invasive varieties of the weed that are commonly found in the country.

1.2 Origin of *Lantana camara*

Lantana camara, originally from South America, is a composite of many horticultural hybrids and few wild lantana species (Sanders 2006). It is not considered weedy in its region of origin, although populations are found scattered along roadsides and in open fields (Day et al. 2003). The plant was introduced into the Netherlands by Dutch explorers in the 1600s from Brazil (Stirton 1977). *Lantana camara* was then crossbred in Europe, prior to its introduction as an ornamental to other countries in the Old World. These imported hybrids have consequently become naturalized and continue to hybridize in the field, causing a highly variable polyploidy and complex species (White 1929; Cilliers & Neser 1991), cultivars (Howard 1969), biotypes or subspecies (Swarbrick 1986) or varieties (CSIR 1962).

Globally, more than 650 variety names occur for *L. camara* and these “taxa” vary in flower color, spinyness, leaf shape, toxicity, vulnerability to herbivore attack and ecology (Diatloff & Haseler 1965; Howard 1969; Smith & Smith 1982). In different regions of its naturalized range, it is widely acknowledged that the weedy form of *L. camara* is morphologically distinct, compared with lantana species in its native range (Sanders 2006).

1.3 Ecological and economic impacts of *Lantana camara*

Lantana camara is an effective competitor against native colonizers (Day & Zaluchi 2009), with the potential to disrupt the succession cycle, forcing out native biota leading to decreased biodiversity (Murali & Setty 2001). The allelopathic effects of lantana reduces seedling recruitment of most species under lantana and cause reduction in the growth of mature trees and shrubs (Gentle & Duggin 1997; Day et al. 2003). The structural and floral composition of native communities could be altered (Fig. 1.1) by *L. camara* infestations (Sharma and Raghubanshi 2010). Lantana increases fuel loads, resulting in hot fires that could penetrate into the surrounding rain forest (Humphries & Stanton 1992; Fensham et al. 1994).

Figure 1.1: *Lantana camara* infestation in the field (Tzaneen).

Lantana camara is a major problem in agricultural areas as it forms impenetrable thickets, causes a reduction in yield and impedes harvesting in plantations and perennial crops (CSIR 1962; Habeck 1976; Kamath 1979; Cock & Godfray 1985; Graaff 1986; Holm et al. 1991; Harley 1992; Harley 1992; Swabrick et al. 1998). Expanding thickets lower water quality and obstruct access to water sources (Urban 2010). Lantana has been associated with the poisoning and death of a range of animals including guinea pigs, horses, dogs, sheep, goats, buffalo, cattle and captive red kangaroos (Sharma 1994; Day et al. 2003b). In South Africa, *L. camara* invasions have been linked to decreased invertebrate diversity (Samways et al., 1996) and reduced grazing potential of up to 80% where stands are very dense (Van Wilgen et al. 2008). Lantana is estimated to have invaded more than 2 million ha in South Africa (Bhagwart et al. 2012). The cost of damage in Australia due to lantana was conservatively estimated at more than AUS$924 million/annum (Pimental et al. 2001) whereas potential economic loss of ZAR710/ha/year [US$1 = R12] would arise if uninvaded areas became invaded by the same weed in South Africa (Van Wilgen et al. 2004).

1.4 Current distribution of *Lantana camara*

Lantana camara is established in all but the driest and most frost prone parts of South Africa. Widespread and high-density populations of *L. camara* are largely restricted to the eastern parts of the country (Fig. 1.2) where it invades moist subtropical, warm and temperate areas in KwaZulu-Natal, Mpumalanga, Eastern Cape and Limpopo provinces (Henderson 2001; Richardson et al. 2004; Urban 2010).

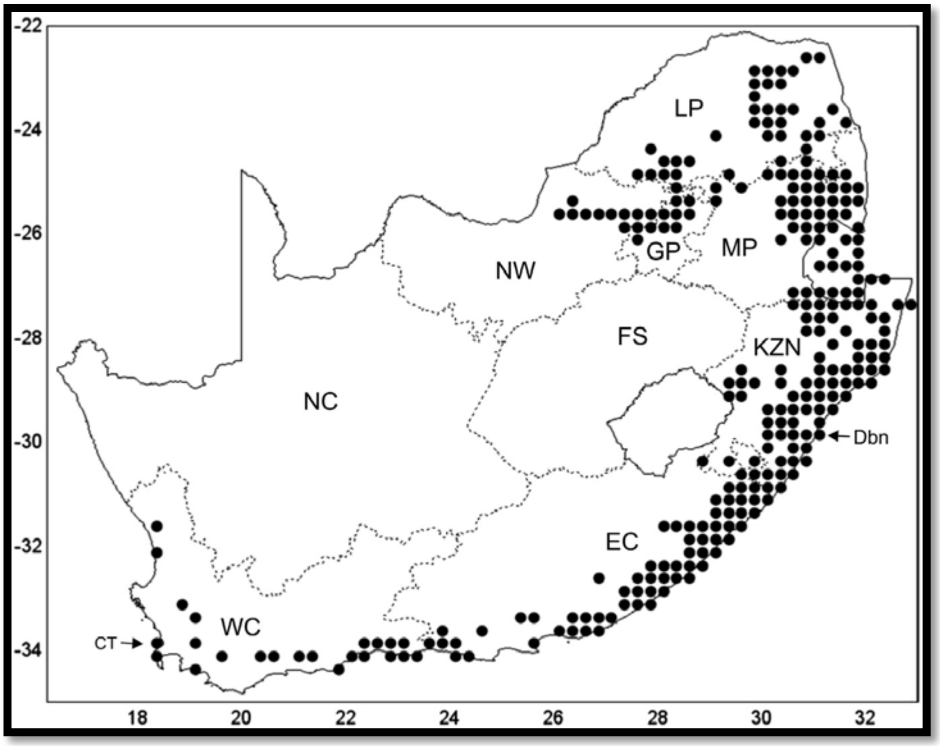

Figure 1.2: Distribution of *Lantana camara* L. (*sensu lato*) in South Africa. (Drawn by L. Henderson. Data source: SAPIA database, Agricultural Research Council-Plant Protection Research Institute, Pretoria).

Although the species is present in the Northern Cape and Free State, no naturalization has been recorded in these regions (Henderson 2001; Henderson 2007). In the Western Cape, *L. camara* is largely restricted to riparian zones (Meek et al. 2010) and areas edging suburban gardens (Alston & Richardson 2006), and these populations are not as dense as in warm and wet regions (Mpumalanga and Kwazulu-Natal).

1.5 Management of *Lantana camara*

In spite of its major economic and ecological impacts in many parts of the world, no standard method has emerged for efficient management of the *L. camara*. This may be as a result of this species occurring across such a wide range of vegetation types and land uses, where human perceptions of *L. camara* as a weed, management goals and available resources differ substantially (Day et al. 2003). Nevertheless, conventional control techniques (i.e., chemical, mechanical and biological control) are practiced.

1.5.1 Mechanical and chemical control

Manipulation and destruction of lantana stands with the aid of machinery and other cultural practices such as hoeing and discing are included under this management practice. Plants also can be removed physically in inaccessible areas such as steep rocky terrain or along creek lines. Physical removal of plants minimizes the disturbance to nearby vegetation, specifically those in minor, isolated clumps growing along fence lines or in public parks. However, mechanical control can be very expensive, and is not viable where land is of low value.

Several chemical compounds have been used for suppression of the invasive *L. camara* (Grobler et al. 2000). In South Africa, imazapyr (Chopper or Hatchet) is among the recommended herbicides, and this is applied on cut stump to inhibit coppice regrowth (Grobler et al. 2000; Urban 2010). Alternatively, broad-leaved spectrum herbicides namely, picloram (Access or Browser) and fluroxypyr/picloram (plenum) could be applied on follow-up treatments as a foliar spray when weed regrowth is at 0.5-1.0 m ht (Grobler et al. 2000; Urban 2010). Chemicals can have non- target detrimental effects on plants and invertebrate species (Urban 2010). Although mechanical and chemical control measures often are applied by land owners in South Africa, these measures are expensive and unsustainable. Regrowth after mechanical or chemical control measures requires expensive follow-up treatments that may involve spot spraying with chemicals or additional mechanical removal.

1.5.2 Biological control

Because conventional control measures such as mechanical and chemical control are not cost effective in controlling invasive plant species, in particular lantana (Khan 1945; Haseler 1963; Willson 1968; Stirton 1977; Scheibelreiter 1980; Thakur et al. 1992), biological control (i.e.

biocontrol), the introduction of selective exotic natural enemies to control exotic pests, is considered as a safe, cost-effective alternative to address this invasive plant problem. The benefits of biocontrol include lack of resistance of the weed to the agent, high benefit: cost ratio for successful programmes, and long-term sustainable management of the target weed species (Van Wilgen et al. 2004). Biocontrol agents often spread throughout the range of the weed population unaided and they can respond to fluctuations in host numbers. Although biocontrol agents do not eradicate weed species such as lantana, their ability to stunt the plants could result in the reduction of seed production, and this could curb the spread of the weed, while allowing some native or pasture species to recover. In comparison to herbicides, biocontrol does not pollute the environment, and is host-specific to a particular target weed species. Although there have been isolated incidents where agents have attacked non-target species, such damage is usually transitory. For example, feeding on *Sesamum indicum* L. (Pedaliaceae) by *Teleonemia scrupulosa* Stål, a leaf-sucking bug released against *L. camara* in Uganda, was reported to be insignificant (Greathead 1973).

Biocontrol programmes for *L. camara* have been ongoing on for over a century in many parts of the world (Perkins & Swezey 1924; Holloway 1964; Greathead 1968; Harley 1974; Cilliers 1983; Neser & Cilliers 1990). The first attempt at biological control was in 1902 in Hawaii through the trial release of 15 insect species (Perkins & Swezey 1924). Since then, lantana biocontrol programmes had been initiated in other parts of the world (Winston et al. 2014), including South Africa, where the programme was started in 1961. Between 1961 and 2011, 26 species of insects were released against *L. camara* in South Africa, and 16 of these are now established (Winston et al. 2014; Cilliers & Neser 1991; Baars & Neser 1999; Klein 2011; Urban et al. 2011; Mukwevho et al. 2017) (Table 1.1). Among the most recent natural enemies that were released against *L. camara* in South Africa during the past 10 years are the root-feeding Mexican flea-beetle, *Longitarsus bethae* Savini & Escalona (Coleoptera: Chrysomelidae: Alticinae), the lantana petiole weevil, *Coelocephalapion camarae* Kissinger (Coleoptera: Brentidae), and the lantana flower gall mite, *Aceria lantanae* Cook (Acari: Eriophydae).

Table 1.1: Established biocontrol agents released for the control of *Lantana camara* in South Africa (Adapted from Winston et al. 2014; Cilliers & Neser 1991; Baars & Neser 1999; Klein 2011; Urban et al. 2011).

Order: Family/ Biocontrol Agent	**Origin**	**Main release (s)**	**Feeding mode**	**Status**	**Damage inflicted**
Acari: Tombiformers ***Aceria lantanae*** **(Cook)**	Mexico	2007 2009 2012	Flower-galler	Established	Extensive, heavy galling in some coastal (KZN) and inland(LP) regions
Coleoptera: Cerambycidae ***Plagiohammus spinipennis*** **(Thompson)**	Mexico via Hawaii via Australia	1973	Stem-borer	Not established	-
Coleoptera: Chrysomelidae ***Alagoasa parana*** **Samuelson**	Brazil via Australia	1985	Leaf feeder	Not established	-
Coleptera: Chrsomelidae ***Longitarsus bethae* Savini &** **Escalona**	Mexico	2007 2012 2013	Root feeder	Established	Unknown or too early for post release
***Octotoma championi* Bly**	Costa Rica via Australia Central America via Australia	1978 1995	Leaf miner	Establishment unconfirmed	Unknown
Octotoma scabripennis **Guérin-Méneville**	Mexico via Hawaii via Australia	1971 1974 1981	Leaf-miner	Establishment in moist, warm eastern range of lantana. Abundant in localized inland areas	Considerable defoliation, but localized
***Uroplata girgadi* Pic**	Paraguay via Hawaii	1974 1983 1984	Leaf-miner	Established, abundant in coastal regions. Present in low	Extensive defoliation in coastal regions

	via Australia			numbers in warm, moist inland areas	
***Uroplata lantanae* Buzzi and Winder**	Brazil via Australia	1984	Leaf-miner	Not established	-
***Uroplata fulvopustulata* Baly**	Costa Rica via Australia	1978	Leaf-miner	Not established	-
Diptera: Agromyzidae ***Calycomyza lantanae* (Frick)**	Trinidad via Australia via Florida (USA)	1982 1989	Leaf-miner	Widely established in low numbers. Heavily parasitized	Slight damage inflicted
***Ophiomyia lantanae** (Froggatt)**	Unknown	1961	Fruit/ seed-miner	Widely established and abundant, but heavily parasitized	Low impact on seed viability
***Ophiomyia camarae* Spencer**	Florida (USA)	2000 2001	Leaf-miner	Widely established	Moderate to considerable
Diptera: Tephritidae ***Eutreta xanthochaeta* Aldrich**	Mexico via Hawaii	1983	Stem/ shoot-miner	Not established	-
Hemiptera: Miridae ***Falconia intermedia* (Distant)**	Jamaica	1999	Leaf-sucker	Establishment in warm, moist areas	Moderate, greatly limited by distribution and population fluctuations
Hemiptera: Tingidae ***Teleonema elata* Drake**	Brazil via Australia	1972	Leaf-sucker	Not established	-
***Teleonemia scrupulosa* Stål**	Mexico via Australia via Mauritius Florida (USA)	1961 1971 1984 1989	Leaf & flower sucker	Widely established in large numbers across the entire range of lantana; severe damage sporadic	Complete defoliation and abortion of flowers in subtropical regions
***Leptobyrsa decora* Drake**	Columbia and Peru	1972	Leaf-sucker	Not established	-
Hemiptera: Ortheziidae ***Orthezia insignis* Browne**	Unknown	1961	Stem & foliage sucker	Widely established	Unknown

				throughout invaded range	
Lepidoptera: Gracillariidae ***Aristea onychote** ()**	Unknown	?	Leaf-miner	Widely established, present in low numbers, heavily parasitized	Unknown
Lepidoptera: Noctuidae ***Hypena laceratalis** Walker**	Kenya and Zimbabwe via Hawaii	1961	Leaf-feeder	Widely established. Larvae are active during summer and autumn and often parasitized	Moderate
***Neogalia sunia* (Guenée)**	California (USA)	1962 1968	Leaf-feeder	Not established	-
Lepidoptera: Pterophoridae ***Lantanophaga pusillidactyla** (Walker)**	Mexico via Hawaii	1961 1984	Flower, fruit and seed chewer	Widely established, but occurs in very low numbers	Unknown
Lepidoptera: Pyralidae ***Salbia Haemorrhoidalis* (Guenée)**	Cuba via Hawaii	1962 1984	Leaf and flower feeder	Widely established in low numbers. Reared from native *Lippia* species	Unknown
Lepidoptera: Tortricidae ***Crorcidosema lantana** Busck**	Hawaii	1961 1984	Flower-peduncle and shoot tip borer	Widely established in low numbers	Unknown
Mycopherellales: Mycopherellaceae ***Passalora lantanae* (Chupp) U. Braun & Crous var *lantanae* (Formerly: Mycovellosiella) [anamorphic fungus]**	Florida (USA)	2002	Leaf spot pathogen	Not established	Unknown

* Insect species present in South Africa prior to deliberate introduction.

Longitarsus bethae, originally collected from Mexico, was introduced into quarantine, because of its ability to damage the root system, a niche not exploited by any of the previously introduced lantana biocontrol agents anywhere in the world. Since its initial release in 2007, *L. bethae* has established in a few sites in South Africa, and the majority of these sites are located along the warm and humid regions in KwaZulu-Natal and Mpumalanga provinces (Table 1.2). Although *L. bethae* is highly damaging on *L. camara* at some of the established sites, it spreads slowly, and is still confined within 2-km radius of the initial release points.

Table 1.2: *Longitarsus bethae* adult release sites where the beetle is established

PROVINCE/SITE	**Coordinates** (Lat/Lon hddd°mm.mmm')	**Number of adults released**	**Date released**	**Distance dispersed from release site** (m)
KZN				
Bizane	31°01.029' S; 30° 06.26' E	60	18/01/2010	450
Port Edward	31°01.198' S; 30° 13.637' E	50	25/10/2011	190
Umzinto	30°15.970' S; 30° 41.862' E	147	25/10/2011	100
Mtubatuba	28°24.981' S; 32° 10.123' E	70	26/10/2011	340
Port Shepstone i	30°43.116' S; 30.17.873' E	1000	29/07/2014	80
Port Shepstone ii	29°46.591' S; 30.45.0760' E	1000	29/07/2014	140
Port Shepstone iii	30°45.837' S; 30.12.177' E	1000	29/07/2014	90
Mkhuze, Sugar cane farm	27°36.143' S; 31.59.766' E	1000	19/09/2014	70
Mpumalanga				
Montenars farm	25°20.870' S; 30.50.097' E	1283	02/10/2009	200

1.6 Rationale and motivation for the study

Despite the importance of below ground herbivores in shaping the structure and function of ecosystems (Masters 2004), our understanding of the ecology underpinning their interaction with other soil-dwelling organisms is limited, compared to those herbivores feeding on aerial parts of the plant. Lantana roots infested with *L. bethae* larvae were often found to be associated with root-knot nematode *M. javanica* (Simelane 2005), a plant-parasite of economic importance in South Africa. Although this was not experimentally proven, Simelane (2005) often observed a positive relationship between the amount of root-galling by *M. javanica* and *L. bethae* performance under laboratory conditions.

Despite the widespread recognition of the relationship between plant-associated insects and root-knot nematodes (Pofu et al. 2012), our understanding of the interface between entomological and nematological research remains limited. Existing research is biased towards aerial parts of the plant, and far less is known about how organisms interact below- ground. Moreover, the interspecific interaction among the soil-dwelling organisms adversaries has seldom been investigated experimentally within the context of biological control. It is likely that the co-existence between *M. javanica* and *L. bethae* facilitates tripartite interactions that could modify plant performance and mortality. Therefore, this study investigated the nature of the relationship between *L. bethae* and *M. javanica*, and determine whether the interaction was synergistic, neutral or antagonistic for the biological control of lantana in South Africa.

1.7 Life history of a root- feeding beetle *Longitarsus bethae*

Longitarsus bethae adults are brown to dark brown with enlarged hind femora, and range from 1.5 to 1.9 mm in body length. *Longitarsus bethae* females are easily distinguished from males because of the swollen abdomen which extends beyond the tip of the elytra, revealing the last three tergites (Simelane 2005). Adult *L. bethae* feed (Fig. 1.3) on the leaves of *L. camara* producing a characteristic pattern of small rough-edged holes. *Longitarsus bethae* adults primarily feed on the mesophyll tissue, but occasionally penetrate the leaf completely. Rarely, adults feed on flower petals (Simelane 2005). Females oviposit within the first 2-cm depth of the soil after a pre-oviposition period of about 10 days (Simelane 2006). Larvae hatch after 10-12 days and feed by excavating cavities in the roots (Simelane 2005). The larvae are white in colour, and they form elongate tunnels within the root. The late stage larvae often feed externally and remove the outer cortex of the rootlets or secondary roots.

Figure 1.3: Damaged leaves of *Lantana camara* (A) and an adult of *Longitarsus bethae* (B).

Similar to other *Longitarsus* species (Ireson et al. 1991; Jordan 1997), *L. bethae* undergoes three larval instars. In potted plants, the beetle pupates mostly within 5 cm of the soil surface and within a 20 cm radius from the root crown. Adult generation time ranged from 52 to 60 days. Preliminary studies showed that the larvae of the insect is highly damaging to the root system, leading to a reduction in the plant growth rate, which also could lead to reduction in flower and seed production (Simelane 2005).

1.8 Biology of a root-knot nematode *Meloidogyne javanica*

Nematodes are small unsegmented worms that live in water, soil, plants and animals (Khan et al. 2008). Root-knot nematodes belong to the genus *Meloidogyne* Göldi, which are highly-adaptable, obligate, polyphagous plant parasites. *Meloidogyne javanica* is distributed worldwide and parasitizes most flowering plants, including economically important crops (Moens et al. 2009). In South Africa, the geographic distribution of *L. camara* (Fig. 1.2) overlaps that of *M. javanica*

(Fig. 1.4); particularly in Mpumalanga, Limpopo, Gauteng and the North West regions where lantana biocontrol is ineffective, due to fewer established biocontrol agents in that region (Kleynhans et al. 1996; Urban et al. 2011).

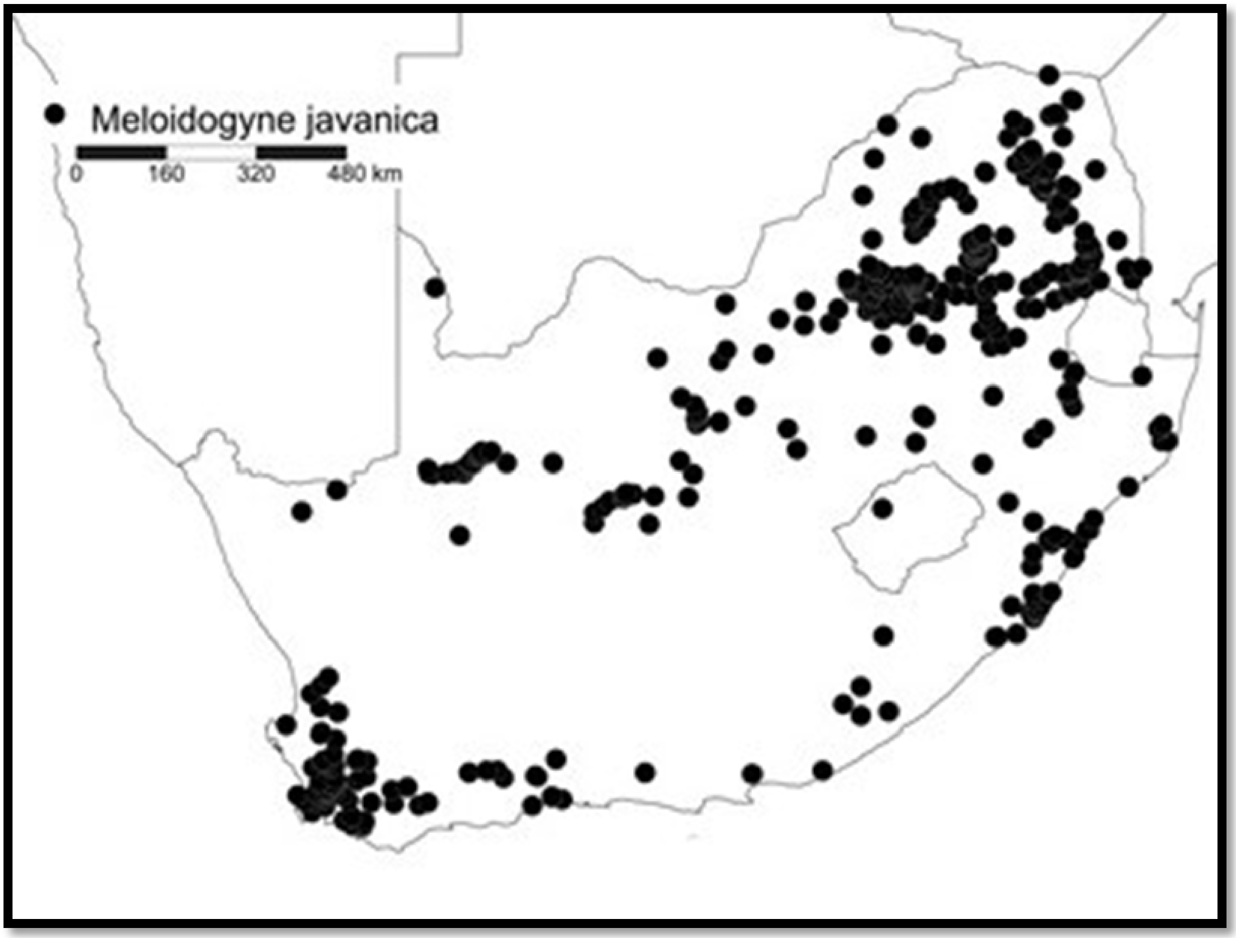

Figure 1.4: Distribution of *Meloidogyne javanica* in South Africa. (Drawn by Mariette Marais. Data source: South African Plant-Parasitic Nematode Survey and National Collection of Nematode and database, Agricultural Research Council-Plant Health and Protection, Pretoria).

A generalized life cycle of *Meloidogyne* root-knot nematodes is summarized in Fig. 1.5. Females deposit eggs into a gelatinous masses composed of a glycoprotein matrix, which is excreted by rectal glands of the female. It holds the eggs together and protects them from environmental extremes and predation. The egg masses are usually found on the external part of galled roots, while they may also be embedded within the gall tissue. The egg mass is initially soft, sticky and hyaline but becomes stronger and dark brown with age (Moens et al. 2009).

Embryogenesis continues to the first-stage juvenile (J1) within the egg, which moults to the infective J2. Hatching of the J2 is mainly dependent upon adequate moisture and temperature. However, other factors including root exudates and growth alter the hatching response so that J2 hatch when conditions are favourable for movement and host location. J2s in the soil often are vulnerable to biotic and abiotic factors and need to locate a host as quickly as possible. J2s are attracted to the roots, and there is evidence that when both resistant and susceptible plant roots are available, the susceptible ones often are more attractive (Moens et al. 2009).

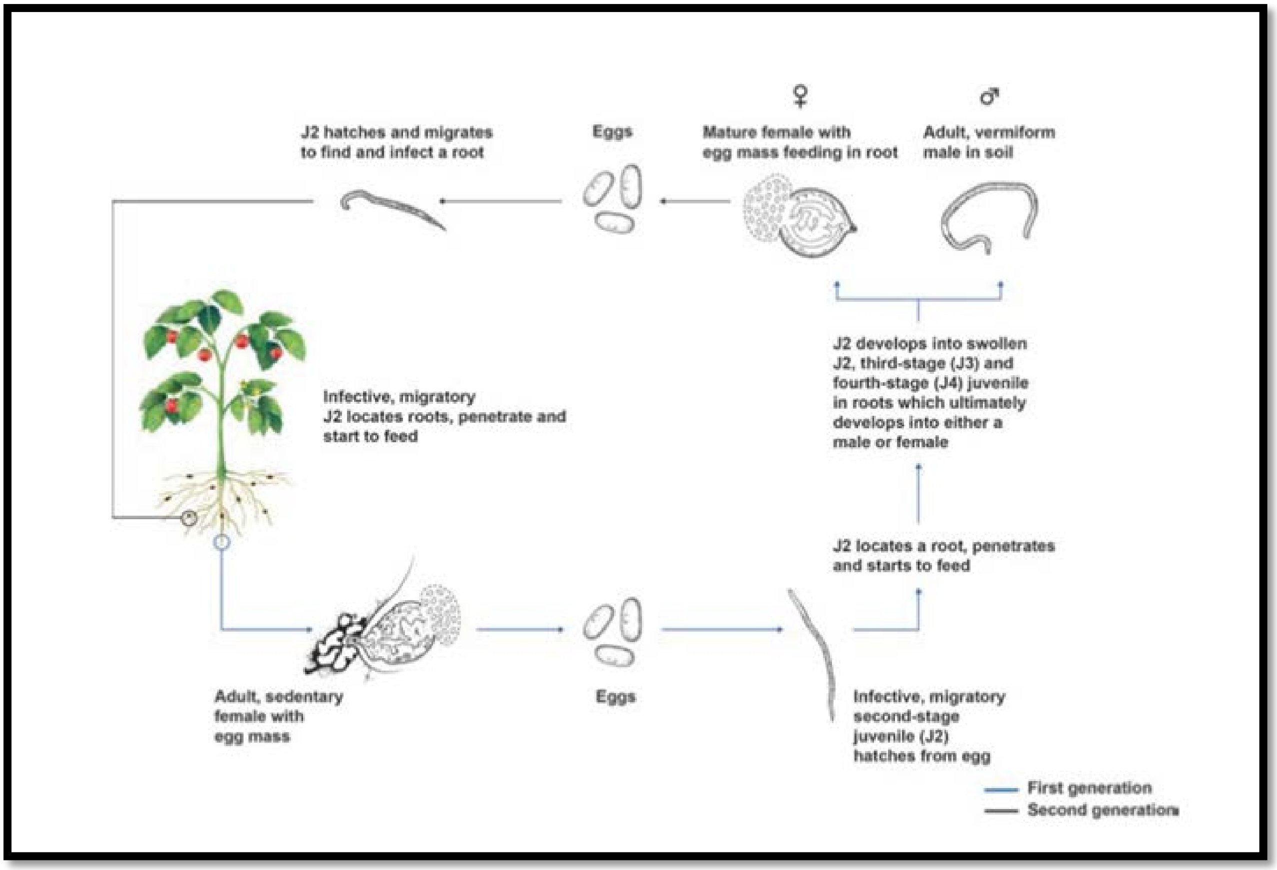

Figure 1.5: Life cycle of *Meloidogyne* sp. (Mashela et al. 2017).

After it has invaded the root, usually behind the root tip, the J2 moves through the root to initiate and develop a permanent feeding site. Protoxylem and protophloem cells are induced to differentiate into specialized nurse cells, which are called giant cells. The nematode becomes sedentary once a giant cell is initiated and enlarges greatly to assume a “sausage” shape. Under suitable conditions, the J2 stage moults to the third-stage juvenile (J3) after 14 days, then to the fourth-stage juvenile (J4), and then finally to the adult stage (Moens et al. 2009).

1.9 Research aims and objectives

The primary aim of the study was to elucidate the interaction between the root-feeding beetle *L. bethae* and the root-knot nematode *M. javanica* with implications for the biological control of *L. camara*.

The specific objectives are:

- i) To determine whether the level of infestation with *L. bethae* increased the likelihood of infection with *M. javanica*.
- ii) To determine whether *L. camara* roots infected with *M. javanica* enhanced the performance of *L. bethae*.
- iii) To compare the single and the combined effect of the two organisms (i.e. *L. bethae* and *M. javanica*) on overall plant (lantana) biomass; and
- iv) To determine the susceptibility of common *L. camara* varieties to *M. javanica*.

CHAPTER TWO

THREE-WAY INTERACTION BETWEEN A ROOT-KNOT NEMATODE *MELOIDOGYNE JAVANICA*, A ROOT-FEEDING FLEA BEETLE *LONGITARSUS BETHAE*, AND THEIR HOST PLANT, *LANTANA CAMARA*

2.1 Introduction

Primary producers in terrestrial ecosystems are predominantly plants, and most other organisms depend on plants for energy and organic material. Plants are important mediators of interactions between their associated microbe and insect communities (Van der Putten et al. 2001; Ohgushi 2005). Changes in plants induced by one species have indirect effects on interactions with other species, thus shaping their abundances (Ohgushi 2008). Although the consequences of such indirect interactions for community structure have predominantly been examined within the plant-associated insect community (Van Zandt & Agrawal 2004; Poelman et al. 2008; April et al. 2010; Utsumi 2011), there is a growing evidence of plant-mediated interactions between microbes and insects (Kluth et al. 2001; Omacini et al. 2001; Katayama et al. 2011; Tack et al. 2012).

Generally, insects and fungi form the two most numerous groups of living organisms in the world, and many individual species of each group utilize higher plants as a food source, and thus it is not surprising that they should interact. Tripartite interaction between insects, pathogens and their host plants can increase the incidence and severity of host injury, thus influencing plant performance and mortality. Various studies and numerous reviews have reported and discussed how such plant parasitic organisms affect each other's performance, reproduction and behavior, and how these are modified by physiological and molecular responses by the plants (De Nooij et al. 1992; Hatcher 1995; Paul et al. 2000; Rostas et al. 2003; Stout et al. 2006; Tack & Dicke 2013).

Root-feeding nematodes are the dominant belowground herbivores, and are mostly regarded as serious pests worldwide. In temperate grasslands they are the main group of root herbivores and their feeding actions can disturb aboveground plant size and nutritional quality (Stanton 1988). whereas several studies have focused on the interactions between root-knot nematodes and aboveground feeding insects (Pofu et al. 2012; Kafle et al. 2017), there have been few studies on the interactions between belowground feeding insects and root-knot nematodes (Dawar et al. 2008; Piśkiewicz et al. 2009; Björsell et al. 2017). Hence, the indirect effects of root-knot nematodes on other soil community members such as root feeding insects are less understood.

By altering interactions with other organisms, root herbivores have the potential to influence plant growth and fitness indirectly (Wootton 1994) and directly through tissue damage (Ohgushi 2005).

Lantana roots infested with *L. bethae* larvae often are associated with *M. javanica* (Simelane 2005), a parasite of various plant species in South Africa (Fourie et al. 2017). Infection by the *Meloidogyne* spp. creates nutrient sinks in susceptible plant species (Verdejo et al. 1988), and this is the case with *L. camara*. If it can be shown that *L. bethae* larval survival is enhanced in *M. javanica*-infected plant roots, this could increase the beetle population and overall plant damage. Although very little is known about the interactions between plant-parasitic nematodes and root-feeding insects, several studies have revealed synergism between root-feeding insects and soil-borne pathogens such as fungi (Leath & Byers 1973; Xixuan et al. 1992; Caeser 2003). For example, a combined effect by the root-feeding beetle *Hylastinus obscurus* Marsham (Coleoptera: Scolytidae) and *Fusarium avenaceum* [(Corda ex Fries) Saccardo] (Hypocreales: Nectriaceae) caused root decline that led to the deterioration of red clover (*Trifolium pratense* L.) (Xixuan et al.1992).

Changes induced by one species in plants have cascading effects on interactions with other species, thus shaping their community structure and abundances (Ohgushi 2008). A synergistic interaction between *Fusarium oxysporum* Schlectend: Fr. and *Rhizoctinia solani* Kuhn, or both fungi with adults and larvae of a flea beetle *Aphthona* spp. caused significantly greater rates of injury to *Euphorbia esulalvirgata* L. than any single agent (Caesar 2003). If the combined effect of *L. bethae* and *M. javanica* provides a synergistic effect on plant damage, there could be an improvement in biological control of *L. camara* in areas where both *L. bethae* and *M. javanica* co-exist.

The objectives of this chapter were to investigate: (i) whether root damage by the root-feeding *L. bethae* enhanced infection by *M. javanica*; (ii) whether *L. camara* roots infected with the nematode *M. javanica* enhanced the performance of the beetle; and also (iii) whether single or combined effect of the two organisms (i.e. *L. bethae* and *M. javanica*) had an overall effect on the growth and biomass of their shared host, *L. camara*.

2.2 Materials and Methods

2.2.1 Quarantine glasshouse conditions

Insect culturing and studies reported in chapters two and three were conducted in a quarantine glasshouse compartment under the following conditions. The compartment had natural lighting supplemented from autumn to spring with quartz-halogen floodlighting for a photoperiod of 14:10 (L: D) h throughout the study period. Atmospheric humidity ranged between 60 and 90% RH. Temperature was controlled by large air-conditioners and maintained at 28 ± 2 °C during the day and 22 ± 2 °C at night throughout the study.

2.2.2 Insects cultures

Longitarsus bethae from Mexico was reared on potted *L. camara* plants of variety light pink 009 LP in accordance with the rearing techniques developed by Simelane (2006). One hundred unsexed *L. bethae* adults were confined with one plant in a gauze- covered cage (0.55 x 0.55 x 0.95 m) during the oviposition period. Adults were allowed to feed and oviposit on each plant for up to 50-62 days before they were transferred to new ones. To keep the soil moist, plants were watered on a daily basis, thus preventing egg desiccation whilst facilitating larval mobility in the soil. Variety light pink 009 LP was used in all the experiments, because it is the most widespread and most common in South Africa.

2.2.3 Rearing of *Longitarsus bethae* eggs

To mass-rear *L. bethae* eggs, a group of 600 adults was enclosed into a gauze-covered cage (0.55 x 0.55 x 0.95 m) with a single potted plant grown in a large pot (10 l) for 8 days. Eggs were deposited within a layer of sand that had been laid down at a depth of 3 cm from the soil surface of the potted plant to facilitate egg recovery. Eggs were extracted from the sand using a sieve-floatation procedure (Foster et al. 1979; Simelane 2006). In this procedure, soil was gently washed through a series of three stacked sieves of downwardly decreasing mesh size (1.0 mm, 0.4 mm, 0.2 mm and 0.1 mm). Eggs were collected on the 0.2 mm sieve and were removed from the filtrate using a fine brush.

2.2.4 Propagation of *Lantana camara* plants

Large pots (10 l) were used to transplant single plants that were propagated from shoot-tip cuttings and grown in well-drained, rich medium of silty soil, sandy soil and compost mixed in a ratio of 2:1:1 by volume, respectively. In all experiments, the standard loamy soil described here was used.

2.2.5 *Meloidogyne javanica* cultures

Meloidogyne javanica used in this study was collected from ARC experiment farm (25°35'57.7" S 28°21'46.1" E), Roodeplaat (Gauteng), by Dr K. M. Pofu and was extracted from the roots of maize, sorghum and bean plants. *Meloidogyne javanica* was reared in the glass house on potted *Solanum lycopersicum* H. Karst. (Solanaceae) (tomato) plants of a variety Money Maker. Money Maker was used, because it is known to be susceptible to *M. javanica* (M Mariette, ARC-PHP, pers comm.).

2.2.6 Propagation of *Solanum lycopersicum* plants

Small pots (2 l) were used to transplant single- *S. lycopersicum* (tomato) seedlings that were propagated from seeds and grown in well-drained, rich medium of silty soil, sandy soil and compost mixed in a ratio of 2:1:1 by volume, respectively. When the tomato seedlings reached a height of 15 cm, they were infested with a mixture of adults and second stage juveniles of *M. javanica* suspended in water. The potted plants were maintained by watering them every 2 days for a period of 2 months to allow *M. javanica* to complete its life cycle and for the infected roots to form galls.

2.2.7 Experimental designs

i) Influence of larval population density of *L. bethae* on the ability of *M. javanica* to infect *L. camara* roots

To determine if the population density of *L. bethae* larvae increased the likelihood of infection of *L. camara* roots by *M. javanica*, an experiment was conducted whereby both organisms were manipulated in potted (2 l) *L. camara* plants. To determine different levels of larval damage by *L. bethae* larvae on the ability of *M. javanica* to infect *L. camara* roots, eggs of the beetle were buried in a shallow furrow on the surface of the soil close to the stem base of *L. camara* at densities of 0 (control), 100, 200 and 300 eggs per plant, representing no larva, low-, medium-, and high larval densities, respectively. Each egg density level was replicated five times, with each plant representing a replicate. After 11 days, 5 g of tomato *S. lycopersicum* (variety: Money Maker), root galls were buried into each *L. camara* plant of all four afore-mentioned treatment groups. According to the formula (1000 µg root galls contain 30 *Meloidogyne* females) from Ferris (2018), this was equivalent to 150 *M. javanica* females per plant. After 62 days, when *M. javanica* was presumed to have completed a life cycle in the *L. camara* roots and had formed galls and egg masses, all the *L. camara* plants in all the treatments were uprooted, washed and inspected for the presence of *M. javanica*. To quantify the level of infection by *M. javanica, L. camara* roots were scored using the mass of the galls formed and then we calculated the number of females in the galls per plant. One-way analysis of variance (ANOVA) was used to compare nematode damage among treatments.

ii) Influence of *M. javanica* infected *L. camara* roots on performance of *L. bethae*

Five *L. camara* plants (Variety 009 LP), grown in (10 l) pots, were infected with *M. javanica* at the inoculation rate of 15 g (450 *M. javanica* females) of the galls per plant. Plants were further maintained for 62 days to ensure the life cycle of *M. javanica* was completed and the galls were formed on the roots. Roots of each *M. javanica*- infected plant were inspected to ensure that all of them are equally infected with the nematode. Each plant was later confined with 50 pairs of *L. bethae* adults in a gauze- covered cage (0.55 m x 0.55 m x 0.95 m) for a period of 55 days. Five healthy (uninfected) plants of the same size also were exposed to the same number of beetles for the same period, and these served as controls. A further set of five plants were only infected with *M. javanica*, and were not infested with *L. bethae*. The parent adults were removed from each plant after 55 days, prior to the emergence of adult progeny. Newly emerged adults were collected and counted on a 2-week interval over a period of 98 days, and comparison of adult emergence between healthy and *M. javanica*- infected plants was made. Performance of *L. bethae* was further quantified by comparing the body size (length and width) and mass of 20 *L. bethae* newly emerged adults emerging from *M. javanica*-infected and healthy plants. T-test for independent grouping was used to compare: number of adults emerging from clean plants, with those emerging from nematode-infected roots; fresh weight (galls) from plants infected with *M. javanica* only and plants infected with both (*M. javanica* and *L. bethae*) organisms and lastly to compare the differences in mass of adults that emerged from clean plants to that of emerged adults from nematode-infected *L .camara* roots.

iii) Single and combined effect of the two organisms (i.e. *L. bethae* and *M. javanica*) on biomass of their host, *L. camara*

To determine the single and combined effect of the two organisms (i.e. *L. bethae* and *M. javanica*) on overall plant biomass, comparison of plant biomass between plants attacked by a single species (i.e. *L. bethae* or *M. javanica*), attacked by both organisms (i.e. *L. bethae* and *M. javanica*) and uninfected (healthy) plants were made. At the end of the experiment described in 2.2.3 (ii), plants were carefully uprooted, and were separated into above- (shoots) and below-ground parts (roots). Soil was removed from the roots by flushing with water. Roots and shoots were put into individual brown paper bags, oven dried at 60 °C for 96 hours, and weighed. ANOVA was used to compare dry biomass of plant shoots and roots of various treatments (Weiß 2007).

2.3 Results

2.3.1 Influence of larval population density of *L. bethae* on the ability of *M. javanica* to infect *L. camara* roots

Gall formation only occurred at the highest *L. bethae* egg inoculation of 300 eggs per plant. No galls were formed on plants inoculated with 200 eggs of *L. bethae* and below (Fig. 2.1). Moreover, no galls were formed on any of the control treatment plants.

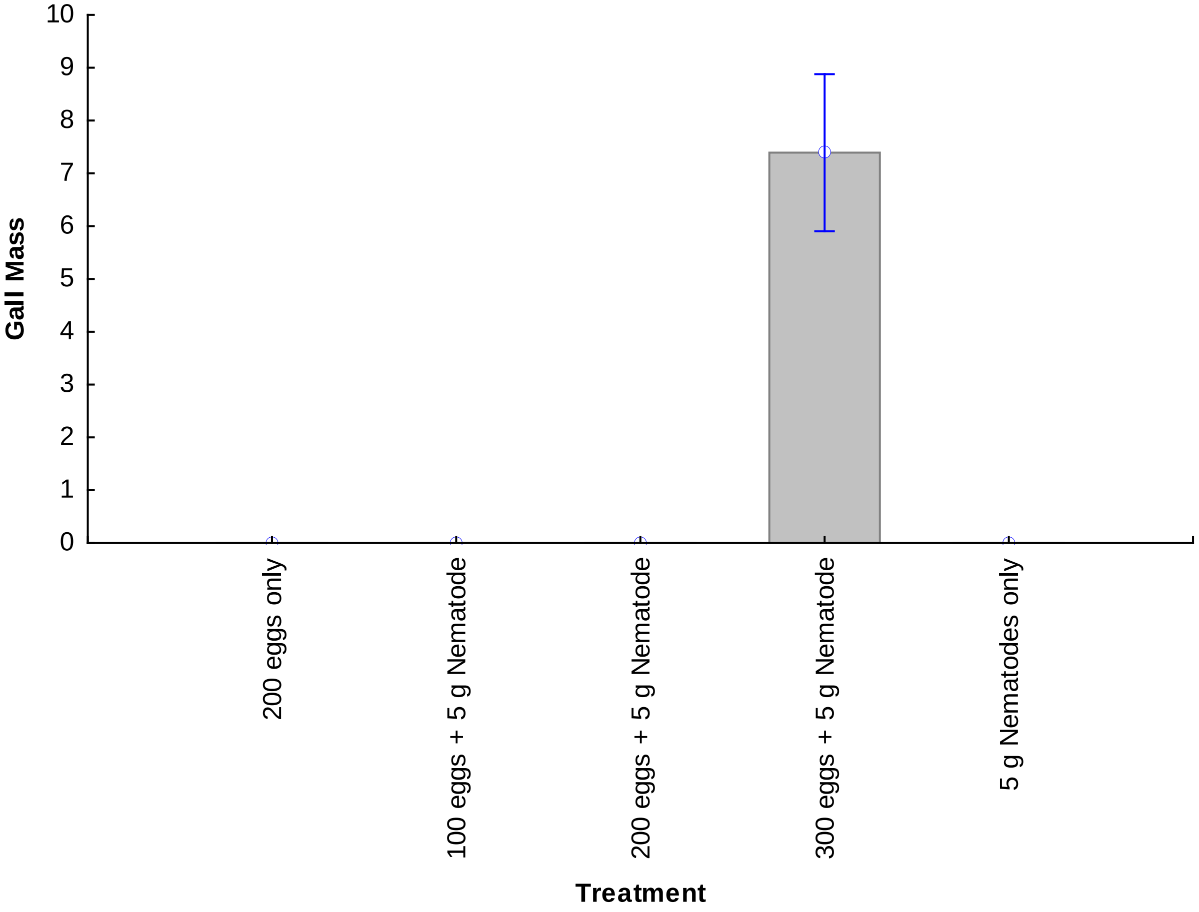

Figure 2.1: *Meloidogyne javanica* damage (mean ± SE) at different larval population densities of *Longitarsus bethae*.

2.3.2 Influence of *Meloidogyne javanica*-infected *Lantana camara* roots on performance of *Longitarsus bethae*

Fifty-five days after exposure of their parents to both healthy and *M. javanica*-infected plants, adult progeny of *L. bethae* started eclosing. Although eclosion of adults from both treatments continued during a 14-week period, more adults eclosed from *M. javanica*-infected than from healthy plants (Fig. 2.2). By the end of the 14-week period, a significantly higher number of *L. bethae* adults had eclosed from *M. javanica*-infected than from healthy plants (*t* = -3.303; *df* = 8; *P* = 0.01) (Fig. 2.3).

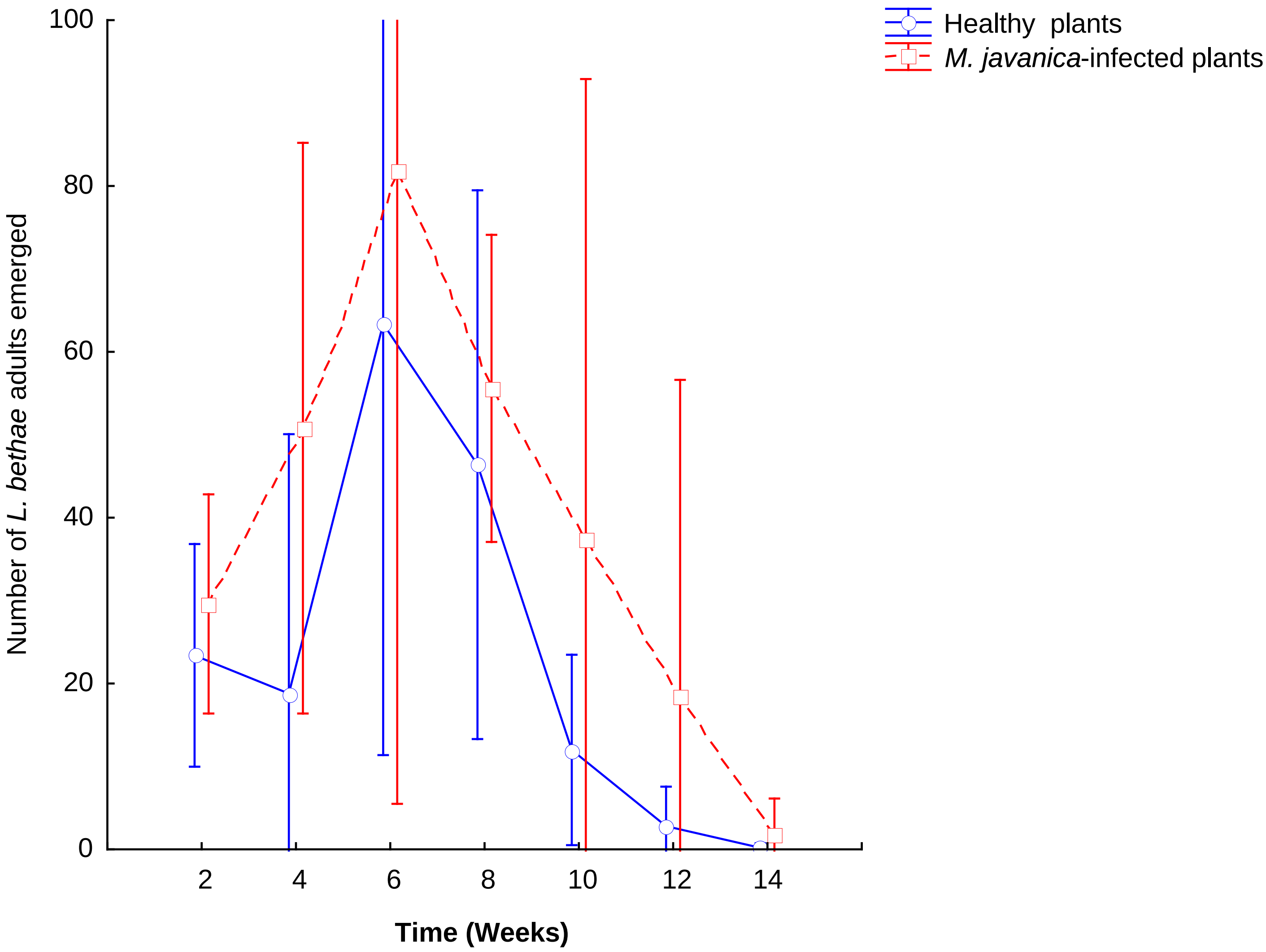

Figure 2.2: Number of *Longitarsus bethae* adults emerging from healthy and *Meloidogyne javanica*-infected plants during a 14-week period.

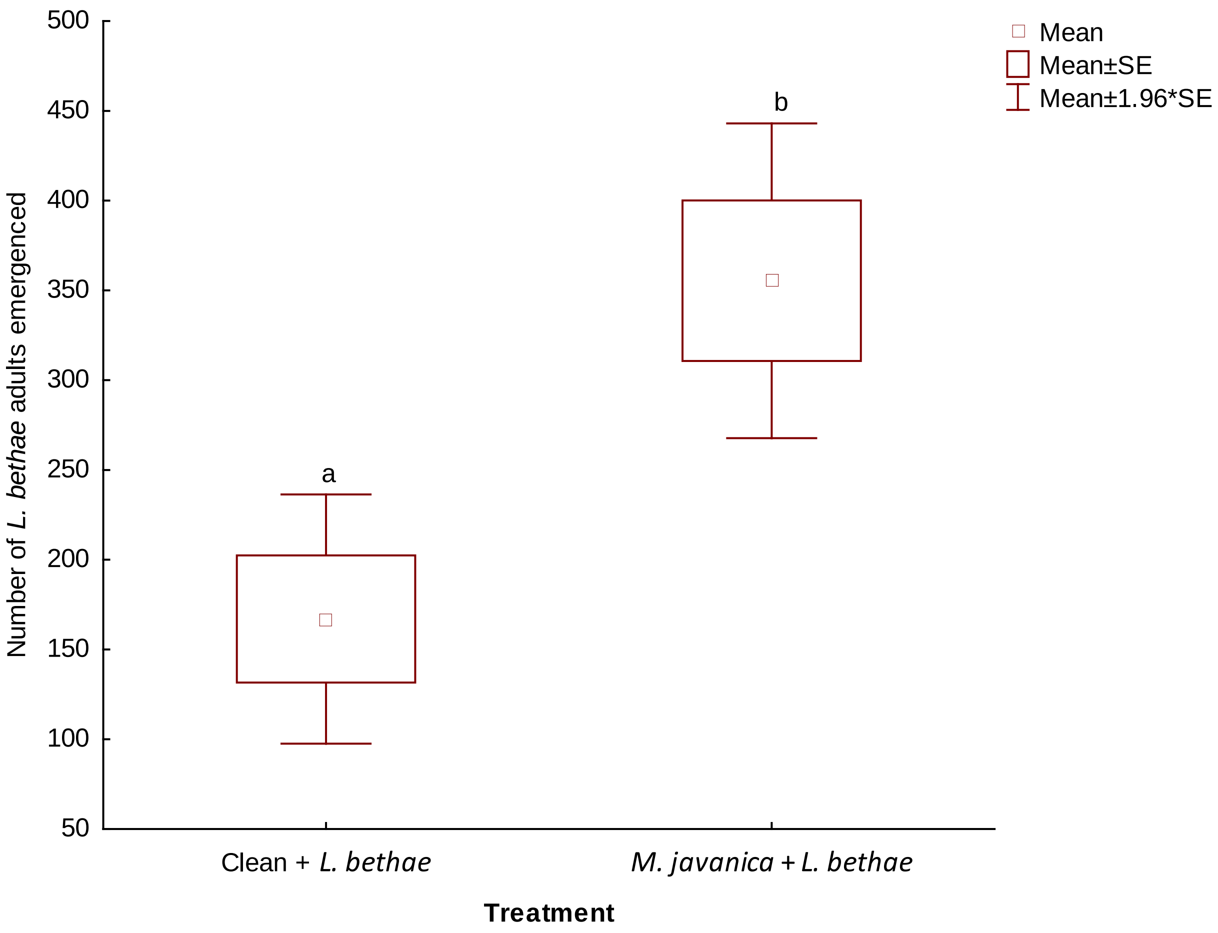

Figure 2.3: Number of *Longitarsus bethae* adults (mean ± SE) emerging from healthy and nematode-infected plants. Means with different letters are statistically different.

Longitarsus bethae adult progeny eclosing from *M. javanica*-infected plants were significantly longer compared to those eclosed from uninfected plants ($t = 3.380$; $df = 8$; $P = 0.009$) (Fig. 2.4). Width of adults eclosing from *M. javanica*-infected plants did not differ statistically from those eclosing from healthy (clean) plants ($t = -2.164$; $df = 8$; $P = 0.06$) (Fig. 2.4). Assuming a 50:50 sex ratio, and that males and females were lumped for measurements, the mass of adults eclosing from nematode-infected and clean plants was almost the same.

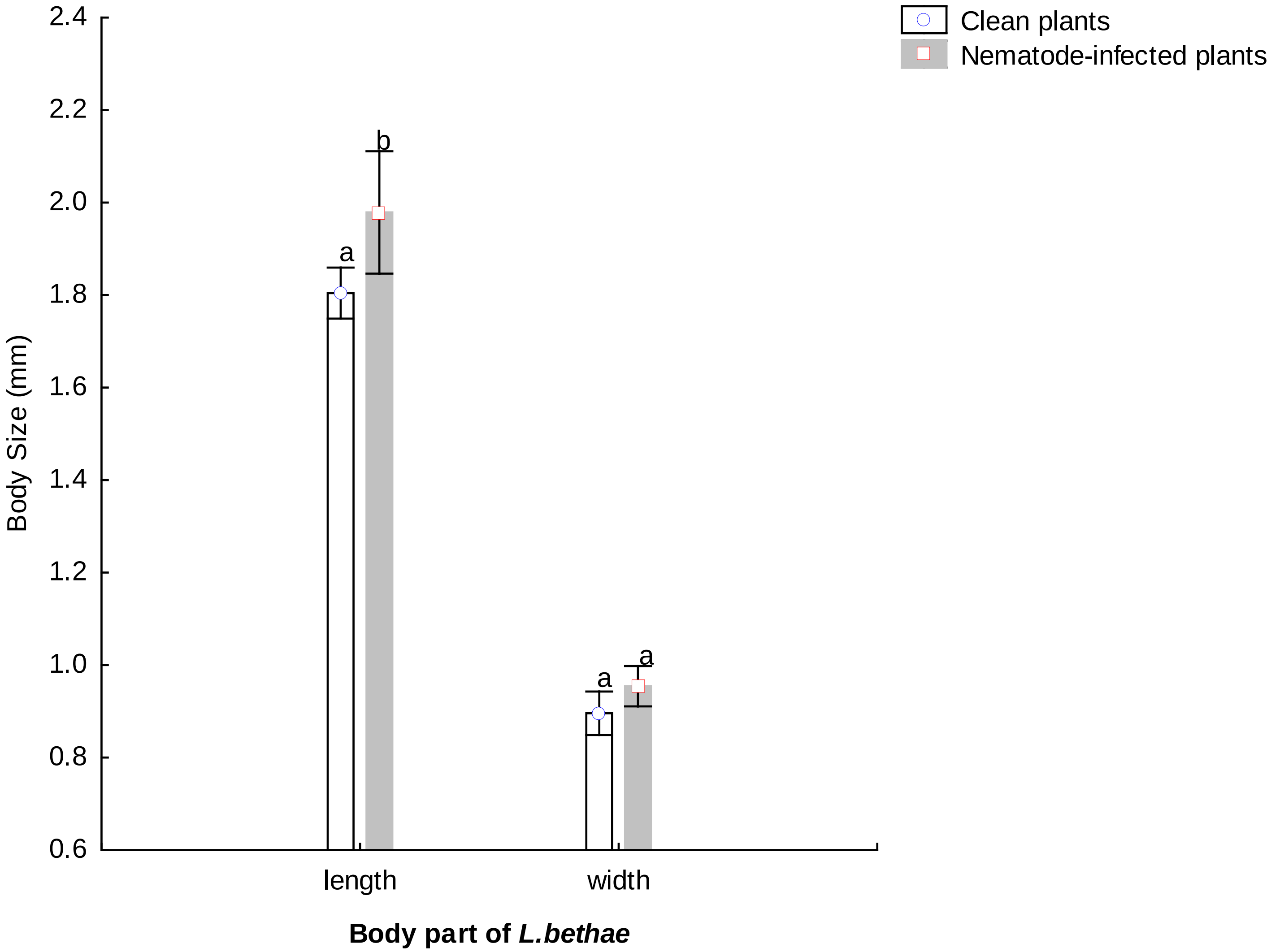

Figure 2.4: Body size of *Longitarsus bethae* progeny reared on healthy and *Meloidogyne javanica*-infected plants (mean ± SE). Means with different letters within the same parameter are statistically different ($P < 0.05$).

2.3.3 Effect of herbivory by either single (*Longitarsus bethae* or *Meloidogyne javanica*) or combined (*L. bethae* plus *M. javanica*) organisms on plant biomass

Gall fresh weight of plant roots that were attacked by a combination of two species (i.e., *L. bethae* and *M. javanica*) was significantly higher than that attacked by *M. javanica* only (F = 5.172; df = 8; P = 0.05), indicating that combination of both species induces more galling than the nematode does alone. The gall fresh weight (mean ± SE) of plant roots that were attacked by a combination of two species (i.e., *L. bethae* and *M. javanica*) was 302.9 ± 28.8 g versus 222.2 ± 21.4 g of that attacked by the nematode *M. javanica* only. There were statistical differences in above-ground (shoot) dry biomass among the treatments ($F = 39.685$; $df = 16$; $P < 0.001$), and that the combined effect of both species and that of nematode alone was significantly greater compared to that of *L. bethae* only. At the end of the experiment, the above-ground dry biomass of plants with *M. javanica* only; *L. bethae* only; and a combination of *M. javanica* and *L. bethae* was 50 %; 22 % and 61 % lower, respectively, than those of control plants (Fig. 2.5). There also were statistical differences in below-ground (root) dry biomass among treatments ($F = 18.561$; $df = 3, 16$; $P < 0.001$), with a singular treatment of nematode *M. javanica* causing the highest reduction in below-ground biomass than the combined and singular treatment of *L. bethae*. The below-ground biomass of plants with *M. javanica* only; *L. bethae* only; and *M. javanica* combined with *L. bethae* was reduced by 45%, 29% and 31%, respectively (Fig. 2.5).

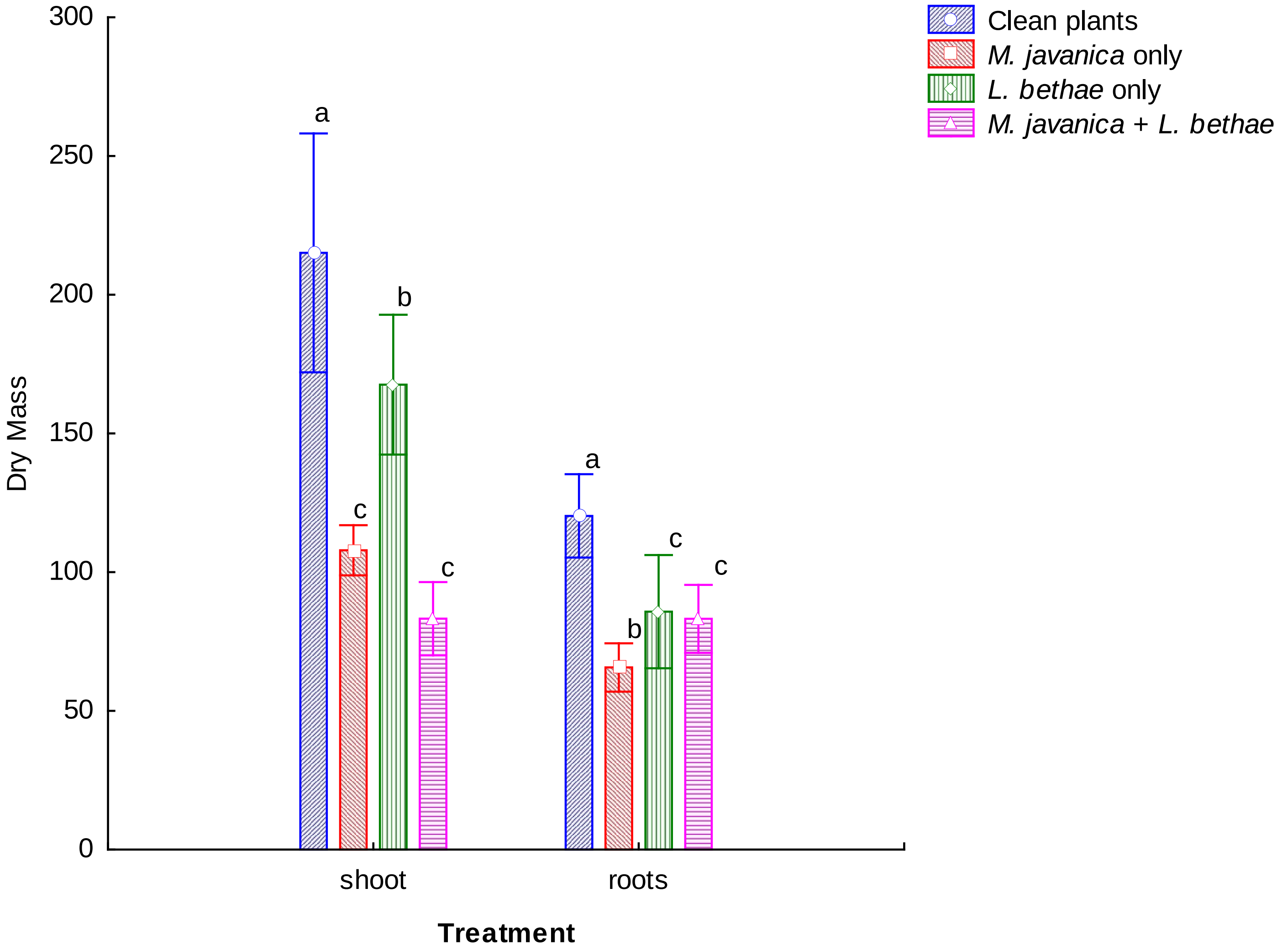

Figure 2.5: Below- and above-ground dry biomass (mean ± SE) of plants with *Meloidogyne javanica* only; *Longitarsus bethae* only and a combination of *M. javanica* and *L. bethae*. Different letters within a plant parameter indicate statistically differences (P < 0.05).

2.4 Discussion

The study showed that galling by *M. javanica* occurs at the highest inoculation of 300 eggs of *L. bethae* per plant, and no galling occurred at inoculation of 200 eggs per plant or less. Galling also did not occur on control plants, which had been infected with the nematode only. Although there is a possibility that high larval density of *L. bethae* may have facilitated invasion by *M. javanica*, it is also likely that infection by the nematode may have been influenced by plant age and the environment (Barker 1976). Plant age cannot be ruled out as actively growing young (< 6 months old) *L. camara* plants similar to those used in the current study were tolerant to *M. javanica* compared to the old (> 12 months old) ones which were often found to be heavily infected with *M. javanica* under nursery conditions(D.O. Simlenae, ARC-PHP, pers comm.). It is unknown what triggered the infection of old plants by *M. javanica* as they had not been pre-exposed to *L. bethae* larval feeding. However, this is not surprising as root-knot nematodes are obligate plant-parasites that can predispose the infected plants to secondary invasion by fungal pathogens and aggravate the disease severity (Sankari Meena et al. 2016). According to Mai & Abawi (1987) most of the soil-borne diseases are influenced by other associated biotic (e.g., other microorganisms, plant age, plant variety.) and abiotic factors (e.g., soil type, temperature.).

This study also showed that *L. bethae* performed better on *M. javanica*-infected than on healthy *L. camara* roots, and that more *L. bethae* adult progeny with slightly bigger body size emerged from *M. javanica*-infected than from healthy plants. The results are consistent with that of Larson & Whitham (1991) and Inbar et al. (1995) who found that herbivores that aggregate locally with the inducers at the site of the nutrient sink can benefit tremendously from the enhanced levels of assimilates. Montandon et al. (1993) found that sap-feeders occurring in close proximity with a nutrient sink, experienced enhanced growth, body size and the survival. Although *L. bethae* is established at some sites in South Africa, it has proven to be a very slow disperser, and is still confined within the 300 m-radius from their original release points (D.O. Simlenae, ARC-PHP, pers comm.). Therefore, the improved performance of *L. bethae* on *M. javanica*-infected plants should result in rapid population growth for the root beetle, and this is likely to increase herbivore pressure on the weed (*L. camara*) over time, while accelerating the beetle's dispersal rate.

Fresh weight (galls) of plant roots from treatments where both species (i.e., *L. bethae* and *M. javanica*) were combined was significantly higher than that from plants infected with the nematode (*M. javanica*) only, suggesting that the combination of both species induces more galling than the nematode does alone. Although not significant, an increase in galling by the two species was associated with a slight reduction in shoot dry weight. The increase in nutrient sink, as demonstrated by an increase in gall weight and the reduction in shoot dry weight, is a reflection of additive herbivore pressure exerted by both species, and this could benefit biocontrol of *L. camara* in areas where the species co-occur. The above-ground dry biomass was significantly lower both in combined and *M. javanica* only treatments than in *L. bethae* only treatment, suggesting that the combination of two species and nematode only caused greater damage than *L. bethae* does alone. Overall, the results of the current study demonstrate that the two species have the potential to complement one another, and fit expectations of the cumulative stress hypothesis (Müller-Schürer & Schroeder 1993; McEvoy & Coombs 1999). The cumulative stress hypothesis states that a combination of biocontrol agents may have a more harmful impact on individual plants, and therefore has the potential to improve biological control.

Although there are a number of examples in the literature where two or more biocontrol agents have had an additive impact on the weed (Knochel et al. 2010; Tipping et al. 2008; Masters and Brown 1992; Simelane & Phenye 2005), studies on the interaction between root-knot nematodes and introduced root-feeding insect agents are rare. Therefore, the potential of nematode species, such as *M. javanica* to enhance and complement introduced root-attacking agents warrants further investigation. Given that below ground plant parts, including rhizomes, storage organs, vascular roots and root buds comprise 50 – 90% of total plant biomass (Andersen 1987, Bazzaz et al. 1987), root-attacking herbivores have a tremendous potential to contribute to weed biocontrol. Barber et al. (2015) reported that direct effect of root herbivory on plants is the most likely driving force behind reduction in plant performance. Therefore, to improve our understanding of root-knot nematode-root insect interactions, joint effort of research disciplines should investigate such interactions from molecular to ecosystem level.

Under field conditions, the positive interaction between *M. javanica* and *L. bethae* will also depend on the susceptibility of *L. camara* varieties. The susceptible variety (009 Light Pink) used in the current study is one of approximately 600 varieties of *L. camara* developed worldwide (Broughton 2000; Day 2012), with over 40 of these in South Africa (Spies & Stirton, 1982; Graaff, 1986). The development of novel genotypes of *L. camara* for horticultural purposes, through the hybridization of different *Lantana* species and varieties has inadvertently improved the plant's resistance to natural enemies (Gentle & Duggin 1997; Stirton 1977; Simelane 2006). Because of varietal resistance, the establishment and performance of introduced biocontrol agents have been adversely affected in several countries, including South Africa (Zalucki et al. 2007; Urban et al. 2011; Day 2012). Therefore, the study in Chapter three is aimed at determining the susceptibility of the most common *L. camara* varieties in South Africa to *M. javanica.*

CHAPTER THREE

SUSCEPTIBILITY OF SELECTED *LANTANA CAMARA* VARIETIES TO THE ROOT-KNOT NEMATODE *MELOIDOGYNE JAVANICA* UNDER GLASSHOUSE CONDITIONS

3.1 Introduction

Hundreds of phenotypes and polyploids of *L. camara* were produced for cultivation as ornamental plants worldwide through deliberate hybridization with other entities, for more than a century outside its native range, with up to 40 varieties occurring in South Africa alone (Graaf 1996). Suitability of the new varieties for the natural enemies that co-evolved with the parental genotypes in their native range has been reduced significantly because of these genetic changes. Incompatibility between some lantana genotypes and the introduced biological control agents often has been reported as the reason for failure of lantana biocontrol programmes in many countries around the world, including South Africa (Harley et al. 1979; Cilliers 1983; Neser & Cilliers 1989; Cilliers & Neser 1991; Day & Neser 2000).

The nutritional quality of plants in nature varies naturally between plant species and also amongst varieties (Van Emden 1987). Larval and nymphal performance and female reproductive output of herbivorous insects is influenced by this variation (Awmack & Leather 2002; Kaspi et al. 2002). For example, development and reproductive life history traits of the European grapevine moth, *Lobesia botrana* [Denis & Schiffermüller] (Lepidoptera: Tortricidae) were strongly affected by grape *Vitis vinifera* L. (Vitaceae) varieties used as larval food sources, and larval development time varied significantly among cultivars/ varieties (Moreau et al. 2006). Gypsy moth (*Lymantria dispar* L. Erebidae) caterpillars reared on white oak, *Quercus alba* L. (Fagales: Fagaceae) foliage developed quicker and produced larger pupae than those fed on willow oak, *Quercus phellos* L. (Barbosa et al. 1983).

Biocontrol agent preference for *L. camara* varieties has resulted in variable success of the biocontrol programme against the weed in South Africa (Harley et al. 1979; Cilliers 1983; Neser & Cilliers 1989; Cilliers & Neser 1991; Baars & Heytek 2003) and Australia (Broughton 2000; Day & Neser 2000). In South Africa, Australia, Fiji, Guam, Hawaii and Micronesia, a decline in the effectiveness of the lantana lace bug *Teleonemia scrupulosa* Stäl (Hemiptera: Tingidae) was found to be associated with the number of established lantana varieties, some of which were poor hosts (Harley et al. 1979; Neser & Cilliers 1989; Denton et al. 1991). Cilliers & Neser (1991) argued that the incompatibility between the gall-forming tephritid fly *Eutreta xanthochaeta* Adrich (Diptera: Tephritidae) and the South African lantana varieties was responsible for the failure of the insect to establish in South Africa. The reproductive performance of the mirid *Falconia intermedia* Distant (Hemiptera: Miridae) varied by up to 20-fold between *L. camara* varieties (Urban & Simelane 1999). Repression of reproductive capacity of lantana by the eriophyd mite *Aceria lantanae* Cook (Trombidiformes: Eriophyidae) varied significantly among lantana varieties, ranging from 10 to 95% between the South African varieties, and from 0 to 30% among the Australian varieties (Urban et al. 2004). On the other hand, in South Africa (Baars & Heytek 2003) and Australia (Broughton 2000), at least five of the 16 established biocontrol agents have established on a wide range of lantana varieties.

Fouri et al. (2012) studied variation in host suitability to root-knot nematode populations in commercial tomato varieties and they found that egg masses and J2 of *Meloidogyne incognita* (Kofold & White) and *M. javanica* were present, and eggs were extracted from the roots of all the varieties included in the study. However, Pofu et al. (2010) found there were statistical differences among Fibre hemp, *Cannabis sativa* L. (Rosales: Cannabaceae) cultivars, for initial and final nematode numbers, whereas Fibre hemp cultivar Futura 75 had the highest number of initial nematodes, and Felina having the lowest initial nematode numbers, cultivars Kompolti and Futura had the highest final nematode numbers. Aung et al. (1990) discovered that production of eggs by *M. incognita* on roots of different maize (*Zea mays* L. (Poaceae) varieties varied with the plantings; the variety and planting date interaction was significant for both reproduction and eggs per gram of root. To determine the potential contribution of the nematode *M. javanica* to *L. camara* biocontrol in South Africa, it is imperative to determine its ability to infect the invasive varieties of the weed that are commonly found in the country. Therefore, this study was conducted to determine the susceptibility of ten *L. camara* varieties that are commonly found in South Africa. In this experiment, *L. camara* variety 009 LP was used as a control because of its high susceptibility to *M. javanica* (see Chapter 2), and it is the most widespread variety in South Africa (Simelane 2006).

3.2 Materials and Methods

3.2.1 Planting of *Lantana camara* varieties

The 10 *L. camara* varieties used in this study are the most common in South Africa (Table 3.1). Single plants were propagated from shoot-tip cuttings and then grown in well-drained sandy soil using 2-L pots. Cuttings were left in the 2- litre pots until they started to develop roots and reach a height of 15 after which they were actively growing and ready to be transplanted from 2- to 10- litre pots.

3.2.2 Inoculation procedure of *L. camara* varieties by *M. javanica*

Meloidogyne javanica-infected *L. camara* variety 009 Light Pink cuttings were grown in 2-litre pots with the soil mix containing silty soil, sandy soil and compost mixed at the ratio of 2:1:1 respectively by volume. After 3 months, the nematode-infected (galled) roots were harvested and used for infecting selected *L. camara* varieties.

Table 3.1 Distinguishing features (morphological and inflorescence colour) among the *Lantana camara* varieties used in the study and the localities from where they were collected. Table was adapted from Mukwevho 2015.

***L. camara* varieties**	**Code**	**Distinguishing morphological features**	**Flower colour (young)**[a]	**Flower colour (mature)**[b]	**Area/ Province (Grid reference)**
Total Pink	021 TP	Leaves broad, rough, hairy; Shoot and Stem hairy with big multiple spines.	Yellow[1]; Violet[2]	Dark Pink[1,2]	Hazyview/ Mpumalanga (25º44.509' S; 030º58.790' E)
Dark Pink	010 DP	Leaves small, tough, hairy; Shoot and Stem hairy with small scattered spines; Stem colour maroon and green small scattered spines.	Dark yellow[1]; Dark pink[2]	Orange[1]; Dark Pink[2]	Colbyn/ Gauteng (25º44.218' S; 028º14.783' E)
Dark Pink	018 DP	Leaves small, tough, hairy; Shoot and Stem hairy with small scattered spines.	Yellow[1]; Light pink[2] with white ring.	Dark Pink[1,2]	Rietondale/ Gauteng (25°43.688' S; 028°14.216' E)

White Pink	021 P	Leaves: broad, rough; Shoot and Stem slightly hairy, heavy spines closely packed on four corners.	Yellow[1]; Pink-white[2]	Light Pink[1,2]	Umhlanga/ KwaZulu-Natal (29º42.747' S; 031º03.176' E)
Light Pink	021 WP	Leaves Small, light coloured, slightly hairy; Shoot and Stem slightly hairy, small multiple spines.	White[1] ; Violet-Light pink[2]	Light Pink[1,2]	Dzwerani/ Limpopo (23º02.777' S; 030º24.628' E)
Light Pink	163 LP	Leaves broad, slightly hairy; Shoot and Stem slightly hairy, small multiple spines.	Yellow1 ; Violet-Light pink2	Light Pink[1,2]	Rietondale/ Gauteng (25° 43.993' S; 28° 13.976' E)
Light Pink	165 LP	Leaves broad, slightly hairy; Shoot and Stem slightly hairy with small sparse spines.	White[1] ; Violet-Light pink[2]	Light Pink[1,2]	Ncotshane/ KwaZulu-Natal (27°21.261' S; 031°30.175' E)
Orange Red	015 OR	Leaves small, tough, very hairy; Shoot and Stem very	Yellow[1,2]	Orange-Red[1,2]	New Germany / KwaZulu-Natal

		hairy with small scattered spines.			(29° 48.210' S; 030°53.433' E)
Hawaii Red	017 OR	Leaves small, tough, very hairy; Shoot and Stem very hairy with small scattered spines.	Orange^{1}; Yellow^{2}	Orange Red^{1,2}	Constantia/ Limpopo (23^{o}38.321' S; 030^{o}39.031' E)
White yellow	015 WY	Leaves small, fleshy, shiny; Shoot and Stem slightly hairy with few small scattered spines.	Yellow^{1}; White^{2}	White^{1,2}	N3 White/ KwaZulu-Natal (29^{o}44.490' S; 030^{o}37.595' E)

Superscript letters represent the stage of maturity of the inflorescence (i.e., ^{a} young and ^{b} mature) whereas superscript numbers represent the inflorescence parts (i.e., ^{1} flower throat and ^{2} lobe/ corolla).

3.2.3 Experimental design

Ten *L. camara* varieties (Table 3.1) were evaluated for susceptibility to the nematode *M. javanica* during 2017/18 under glasshouse conditions where *L. camara* variety 009 Light pink variety was used as a source of inoculum of the nematode *M. javanica* as described in 3.2.2 previously.

The root galls of Light Pink 009 LP variety were separated from the shoots, and were cleaned up by flushing with water. The root galls were then weighed to ensure that 25 g of galls were used to infect healthy rooted cuttings of each of the 10 *L. camara* varieties. According to the formula from Ferris (2018), 1000 µg of root galls contain 30 *Meloidogyne* females, and therefore 25 g of root galls is equivalent to 750 *M. javanica* females. Each cutting was grown in a 10-L pot with the soil mix containing silty soil, sandy soil and compost mixed at the ratio of 2:1:1 respectively, by volume, and that all the cuttings were grown on the same soil mix. The infected plants were watered once every second day and rotated on a weekly basis to ensure homogeneous greenhouse light and temperature conditions. The experiment was conducted during the summer season of 2017/18, under greenhouse conditions, at Roodeplaat, Pretoria, where the average minimum and maximum temperatures were 17 ºC and 31 ºC, respectively, and a photoperiod of 14:10 hours (L:D). The *L. camara* varieties were uprooted nine weeks after inoculation, and each plant was carefully inspected for the presence of galls. The galled roots were carefully removed from root system of each plant, washed with water and the fresh weight of galls was determined. The information from Ferris (2018) was used to determine the number of female *M. javanica* per plant and the fresh weight of galls was compared among the 10 *L. camara* varieties.

3.2.4 Statistical analysis

Data were analyzed by one-way analysis of variance (ANOVA) using Statistica version 8 (Weiß 2007). To stabilize the variance, the data were log [log (n+1)]-transformed before being subjected to ANOVA, but untransformed data are presented. The means obtained were separated using Fisher’s protected least significant difference (L.S.D) method at 5% (*P* = 0.05) level of significance.

3.3 Results

All *L. camara* varieties used in this study were infected with *M. javanica*, albeit at varying degrees of infection. The lantana variety Orange Red (015 OR) had the highest fresh gall weight (15.33 ± 3.092 g; mean ± SE) than all other varieties (Fig. 3.1), and according to Yeates (1972), this was equivalent to (460 ± 92.77; mean ± SE) *M. javanica* females per plant (Table 3. 2). Light Pink variety (009 LP), which was used as a control, was the next most susceptible variety to *M. javanica.* Although the gall weight of 009 LP variety was significantly lower than that of 015 OR variety ($F = 9.669$; $df = 40$; $P < 0.05$), it did not differ statistically from those of Total Pink (021 TP) and Dark Pink (018 DP) varieties, and their gall weights ranged between 4 ± 0.21 and 8 ± 1.48 g. White Yellow (015 WY) was the most resistant variety, and had the least fresh gall weight of 0.44 ± 0.273g.

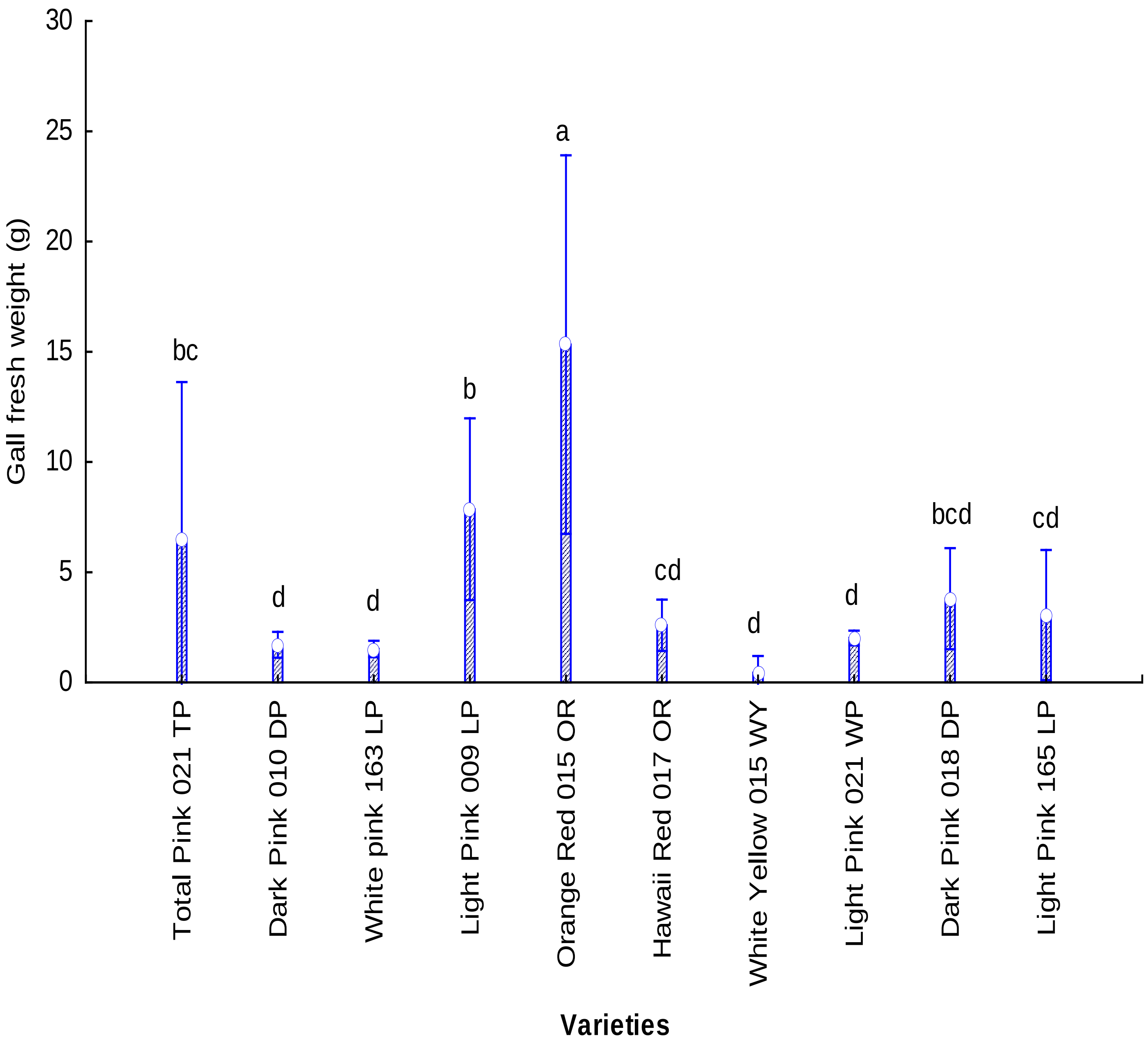

Figure 3.1: Fresh gall weight of different *Lantana camara* varieties post-inoculation with the nematode *Meloidogyne javanica*. Means (±SE) with different letters are statistically different ($P < 0.05$).

Table 3.2 Number of *Meloidogyne javanica* females per *Lantana camara* variety based on the weight of galls per plant using the formula (1000 µg root gall is equivalent to 30 *Meloidogyne* females) from Ferris (2018).

***L. camara* variety**	**Weight of galls per plant (g) (mean ± SE)**	**Number of *M. javanica* females per plant (mean ± SE)**
Total Pink 021 TP	6.51 ± 0.146bc	195 ± 0.146
Dark Pink 010 DP	1.71 ± 0.053d	51 ± 0.053
Dark Pink 018 DP	3.80 ± 0.105bcd	114 ± 0.105
White Pink 163 WP	1.52 ± 0.038d	46 ± 0.038
Light Pink 009 LP	7.86 ± 0.087b	236 ± 0.087
Light Pink 165 LP	3.05 ± 0.102cd	92 ± 0.114
Light Pink 021 WP	2.02 ± 0.115d	2 ± 0.028
Orange Red 015 OR	15.33 ± 0.086a	460 ± 0.102
Hawaii Red 017 OR	2.59 ± 0.028cd	78 ± 0.086
White Yellow 015 WY	0.44 ± 0.017d	13 ± 0.372

Means (± SE) with different letters are statistically different ($P < 0.05$).

3.4 Discussion

Differences in the fresh gall weight among the 10 *L. camara* varieties indicated different levels of susceptibility of the varieties to *M. javanica*; at least one variety (Orange Red 015 OR) ranked in the top grouping. Other susceptible varieties were Light Pink 009 LP, Total Pink 021 TP and Dark Pink 018 DP, and these, together with variety Orange Red 015 OR, constituted 40% of the tested *L. camara* varieties. Fifty percent of the varieties displayed slight to moderate susceptibility to *M. javanica* and 10% displayed lack of susceptibility. Given the variation in the susceptibility of South African *L. camara* varieties to introduced natural enemies (Baars & Neser 1999; Broughton 2000; Reinert et al. 2006; Simelane 2006; Zalucki et al. 2007; Urban et al. 2011; Day 2012; Mukwevho et al. 2017), the variation displayed by the 10 selected varieties to infection by the nematode *M. javanica* is not surprising. Interestingly, variety 015 White Yellow also was the most resistant variety to the flower gall mite *A. lantanae* (Mukwevho et al. 2017), and this is ranked among the most invasive varieties in the low veld regions of Mpumalanga and Limpopo provinces (D. Simelane, Pers. comm).

Susceptibility of the Light Pink variety 009 LP to *M. javanica* bodes well for *L. camara* biocontrol in South Africa as this variety has been ranked as the most common in the country (Simelane 2006; Mukwevho 2017). Light Pink (009 LP) also is susceptible to *L. bethae*, and the beetle is well established at a few sites invaded by this variety in KwaZulu-Natal (D.O. Simlenae, ARC-PHP, pers comm.). Therefore, the positive interaction between the flea beetle and the nematode on variety Light Pink 009 LP (Chapter 2) suggests that high population densities of the beetle can be anticipated at release sites where both species occur. Two biocontrol agents, the lace bug *T. scrupulosa* and the flea beetle *L. bethae*, also have shown a strong preference for variety Orange Red 015 OR (Radunz 1971; Simelane 2006). Although variety 015 OR is not the most common in South Africa, the few sites where this variety co-exists with *M. javanica*, particularly in the low veld region of Mpumalanga and KwaZulu-Natal where the beetle is well established, should be prioritized for evaluation as the control should be excellent. Given the positive interaction between *M. javanica* and the variety Orange Red 015 OR, rapid population growth of the beetle *L. bethae* also should be anticipated at sites where this variety co-exists with *M. javanica*.

Generally, the findings of the current study are in agreement with others that reported genetic variation of various plant species to root-knot nematode infection. For example, Ngobeni et al. (2011) and Fourie et al. (2015) reported genetic variability and host suitability of maize (*Z. mays*) and soybean (*Glycine max* (L.) Merr.) cultivars to the nematode *M. javanica*, respectively. These results, and many others, can be exploited in resistance breeding programmes aimed at developing cultivars that are less susceptible to root-knot nematodes but that would perform optimally in soils conducive to nematode infection.

The suitability of some invasive *L. camara* varieties such as Light Pink 009 LP and Orange Red 015 OR for *M. javanica* and the ability of this nematode to reduce growth of *L. camara* (Chapter 2) should contribute towards biological control of this weed in South Africa. Therefore, sites where suitable varieties co-exist with the nematode should be prioritized for release of the root beetle *L. bethae* whose, fitness is positively influenced by the nematode-infected plants (Chapter 2).

CHAPTER FOUR

GENERAL DISCUSSION

4.1 Nematodes and insect herbivores

In natural ecological systems, plants often are simultaneously attacked by several herbivores. This interaction may affect the performance of the herbivores themselves, and may have varying degrees of impact on their host plant fitness. In this study, the nematode *M. javanica*, as a result of its intimate association with *L. camara* root system, influenced the performance of the root beetle *L. bethae* due to its association with *L. camara* root system, and this resulted in an additive negative effect on biomass accumulation of their mutual host *L. camara*.

Although the study showed that the interaction between *L. bethae* and *M. javanica* on *L. camara* roots improved the reproductive output of the *L. bethae*, it remains unclear as to what development stage of the beetle benefited from the association between the two species. However, it was assumed that *M. javanica*, by changing the quality or the quantity of root resources, positively influenced the performance and survival of *L. bethae* larvae, and subsequently increased the abundance of the beetle. Studies whereby the association between a nematode and an insect herbivore improves the fitness of the latter are rare. However, there are a number of studies that have reported negative correlations between nematode presence and insect population growth. For example, population growth of the aphid *Brevicoryne brassicae* L. (Hemiptera; Aphididae) population growth on cabbage, *Brassica oleracea* L. (Brassicaceae), was reduced on plants infected with the nematode *Heterodera schachtii* Schmidt (Tylenchida: Heteroderidae) 4 weeks prior to aphid infestation (Hol et al. 2013). Similarly, egg density soybean cyst nematode, *Heterodera glycines* Ichinohe (Tylenchida: Heteroderidae), was negatively correlated with colonization by the aphid *Aphis glycines* Matsumura (Hemiptera; Aphididae) on soybean *Glycine max* L. Merr, and that high nematode egg density was associated with a decline in soybean yield (Hong et al. 2011). Pathogen infections often adversely affect the performance of insect herbivores through restricted nutrition and defensive response by their host plants (Hong et al. 2011; Bennett et al. 2013; Gange 2001; Gange et al. 1994).

Results of this study revealed not only the positive effects of *M. javanica* infection on the fitness of *L. bethae*, but also the additive effect of both species on the biomass reduction of their weedy host *L. camara*. Some examples of successful weed biological control are based on this type of interaction. For instance, the success of the Argentine cactus moth *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae), in controlling the invasive prickly pear *Opuntia stricta* (Haw) Haw. (Cactaceae) in the 1920s was partly based on the fact that its feeding wounds provided access to secondary pathogens that killed the cactus (Caesar 2000). Venter et al. (2013) demonstrated that pathogens (fungi and bacteria) associated with the weevil *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae) could reduce water hyacinth *Eichhornia crassipes* (Mart.) Solms Laub. (Commelinales: Pontederiaceae) leaf photosynthetic rate. Moran (2005) also showed that an increase in the population of weevils *N. eichhorniae* and *Neochetina bruchi* Hustache (Coleoptera: Brachyceridae) and the severity of the fungus *Cercospora piaropi* Tharp (Capnodiales: Mycosphaerellaceae) infection resulted in a greater decline in water hyacinth leaf production and plant densities in relation to control plots (Charudattan 2001).

Lantana biocontrol has been characterized by releases of multiple (24) biocontrol agents, 16 of which are now established in South Africa (Mukwevho et al. 2017), and are reported to cause moderate to substantial control of the weed in the humid KwaZulu-Natal coastal regions (Urban et al. 2011). Despite the concern regarding the release of multiple weed biocontrol agents (Louda 1999; Myers and Bazely 2003), this strategy has been necessary for *L. camara* biocontrol worldwide. Given the differential response of natural enemies to over 40 different *L. camara* genotypes (Swarbrick et al. 1998; Urban et al. 2011; Day 2012) in South Africa, the use of a suite of agent species or genotypes of species, sourced from different lantana genotypes in the native range (Baars & Neser 1999; Broughton 2000; Day et al. 2003; Urban et al. 2011; Day 2012), has been the most effective biocontrol strategy for the weed. In the current study, the susceptibility of *M. javanica* also varied significantly among the 10 common *L. camara* varieties found in South Africa, and some were highly resistant to the nematode (Chapter 3). Nonetheless, the improvement in the fitness of *L. bethae* as a result of its symbiotic relationship with *M. javanica* on one of the most common host varieties in South Africa (Chapter 2) and the susceptibility of some invasive varieties to the nematode (Chapter 3), should contribute towards biocontrol of this weed in this country.

4.2. The effect of multiple agents in weed biological control

Root-feeding nematodes are dominant belowground herbivores, and their feeding activities can affect aboveground plant size and nutritional quality (Stanton 1988) and aboveground insects (Bezemer et al. 2005; Simelane 2006; Kaplan et al. 2011). Chapter 2 showed that *M. javanica* can reduce the above ground biomass of *L. camara* variety Light Pink 009 LP, and this could have far-reaching implications on the reproductive output of the infected plants and the fitness of the associated aboveground insects. The fact that over a dozen *L. camara* biocontrol agents are foliage feeders, it is likely that these may be negatively affected due to reduction of the above-ground biomass caused by *M. javanica* infection (Chapter 2), and this warrants further investigation. Irrespective of the consequences of the interaction on their fitness, the ability of *L. bethae* and *M. javanica* to reduce the biomass of *L. camara* will decrease the invasiveness of this weed in South Africa. There are a number of examples whereby the interaction among agents resulted in additive or synergistic reduction on growth of their host plants, and this had contributed to the success of some biocontrol programmes (Hatcher 1995; Crowe & Bourchier 2006; Groenteman et al. 2007; Hoffmann & Moran 1998; Knochel et al. 2010; Turner et al. 2010; Buccellato et al. 2012). For example, the combined effects of concurrent herbivory by a root weevil, *Cyphocleonus achates* (Fåhraeus) (Coleoptera: Curculionidae) and a flower head weevil, *Larinus minutus* Gyllenhal (Coleoptera: Curculionidae), on the biomass and flower production of spotted knapweed *Centaurea stoebe* L. subsp. *micranthos* (Gugler) Hayek were additive (Knochel et al. 2010). Turner et al. (2010) also found that the combination of the two agents, the rust fungus, *Puccinia mysiphylli* (Thuem) Winter (Pucciniales: Pucciniaceae) and an undescribed leafhopper (Tribe Erythroneurini), formerly referred to as *Zygina* sp., had a greater effect in the control of bridal creeper *Asparagus asparagoides* L. Druce (Asparagoideae) than each of them individually. The invasiveness of *L. camara* can be attributed to its prolific seed production, and therefore a suit of natural enemies that impact directly or indirectly on the plant's sexual reproduction fecundity would be of great benefit for the long-term management and containment of this weed.

Because of the combined below-ground herbivory by both *M. javanica* and *L. bethae,* other complex interactions among above-ground lantana biocontrol agents are likely to emerge. For example, the study by Simelane (2006) found that *Teleonema scrupulosa* Stäl (Hemiptera:

Tingidae)-infested plants reduced survival *L. bethae* larvae, and that plants infested by the leaf bug were avoided as oviposition sites by adult beetles, while those that were less infested with *T. scrupulosa* were frequently chosen and provided better conditions for beetle larval survival. Therefore, it would be interesting to evaluate the consequences of the interactions between below- (i.e., *M. javanica* and *L. bethae*) and above-ground herbivores of *L. camara* at both molecular and ecosystem levels. A better understanding of these biological processes would help in approaches aimed at conserving beneficial interactions that can contribute towards biocontrol of *L. camara*. However, because soils are complex and heterogeneous ecosystems, the application of various strategies cannot be generalized for belowground herbivores, and will have to be carefully assessed in case by case studies. Simelane (2007) found that *L. bethae* performs much better on moderately moist clay than on sandy soils, and thus a change in soil conditions might have unexpected consequences on its interaction with other species.

With the exception of a few field studies (Hong et al. 2011; Mao et al. 2011), the majority of pathogen-insect interaction studies, including the current study, were conducted on potted plants (Gange & West 1994; Gehring et al. 1997; Chow et al. 2018), making it difficult to predict with certainty the outcome of the interaction among species under field conditions. Thus, additional studies that directly manipulate nematode abundance and use larger field plots should be conducted using larger field plots in order to better elucidate *L. bethae-M. javanica* interactions. As Raghu et al. (2006) & Morin et al. (2009) showed in their respective studies, laboratory studies might underestimate the long-term impact of the interacting herbivore species on *L. camara*. For example, the efficacy of the mealybug, *Hypogeococcus festerianus* (Lizery Trelles) (Pseudococcidae) released as a biological control for harrisia cactus, *Harrisia martinii* (Labour.) Britton & Rose (Cactaceae) was much greater in the field than what was predicted from laboratory-based studies (McFadyen & Tomley 1981).

4.3. Implications for the biological control of *Lantana camara* in South Africa

Inasmuch as *M. javanica* can reduce growth of susceptible lantana varieties, its utilization as a biocontrol agent for *L. camara* should be done with caution as the nematode is a major pest of a number of crop species worldwide. Because plant species that are susceptible to root-knot nematode species can act as reservoir hosts of pests (Kaur et al. 2007; Lavinia 2016; Ntidi 2008; Tedford et al. 1988; Singh et al. 2010), growing nematode-susceptible *L. camara* varieties near agroecosystems where susceptible crop species are also grown is not recommended. Nematode-infected weeds allowed to decompose in the field can facilitate its spread to non-infected areas when infected weed rootstock is blown or washed to other farms (Singh et al. 2010). *Meloidogyne javanica*-infected varieties/populations of *L. camara* should only be targeted for the release of the beetle at sites located in natural ecosystems, rather than near agroecosystem where susceptible crop species are likely to be infected. To exploit the improved fitness of *L. bethae* on *M. javanica*-infected plants, the nematode also could also be used for mass-rearing of the beetle under insectary conditions. These strategies not only will maximize the number of robust *L. bethae* adults released, but would also facilitate the redistribution of the beetle to other sites infested by the weed.

Although this study found that some *L. camara* varieties were susceptible to *M. javanica*, it is confusing that a number of other studies have reported nematicidal effect of *L. camara* to *Meloidogyne* spp. (Ali et al. 2001; Al-banna et al. 2003; Radwan et al. 2007; Ahmad et al. 2010 ; Chedekal 2013), including *M. javanica* (Radwan et al. 2007). Shaukat et al. (2003) showed that *L. camara* roots contain weak enzymatic hygrogen cynide. High concentrations of HCN in a plant growth promoting bacterium (PGPB), *Pseudomonas aeruginosa* Migula (Pseudomonadales: Pseudomonaceae), have been found to be the primary factor that kills nematode (Gallagher & Manoil 2001). Given the effect of genetic variability of *L. camara* on susceptibility to *M. javanica*, it is possible that some resistant *L. camara* varieties such as White Yellow (015 WY) could have elevated concentrations of HCN that may be detrimental to the nematode. Indeed, different rootstocks or germplasms of the same crop species could display a wide range of resistance to a particular root-knot nematode species (Barker & Olthof 1976; Ruponnois et al. 1999; Cervantes-Flores et al. 2002; Mwangi et al. 2015), and those resistant genes could be used for developing commercial cultivars. For example, Fourie et al. (1999) studied the host suitability of South African commercial soybean cultivars to two root-knot nematode species and reported substantial variation among 38 soybean cultivars with regard to host suitability for *M. javanica* and *M. incognita* races.

4.4 Conclusion

In conclusion, the symbiotic relationship between the flea beetle *L. bethae* and *M. javanica* appears to be commensal, resulting in the increase in fitness of the beetle. The combined herbivory by *L. bethae* and *M. javanica* is additive on one of the most common varieties of *L. camara* in South Africa, and therefore co-infestation by both species might enhance the biological control of this weed in South Africa. Interaction between *L. bethae* and *M. javanica* under field conditions, and other complex interactions that may arise as result of below-ground herbivory by both species need to be investigated further.

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