ESTABLISHMENT AND IMPACT OF THE SAP-SUCKING MIRID, *FALCONIA INTERMEDIA* (DISTANT) (HEMIPTERA: MIRIDAE) ON *LANTANA CAMARA* (VERBENACEAE) VARIETIES IN THE EASTERN CAPE PROVINCE, SOUTH AFRICA

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

MASTER OF SCIENCE

of

RHODES UNIVERSITY

by

UNATHI-NKOSI LELETHU PETER HESHULA

January 2005

Abstract

The biological control of the weedy complex *Lantana camara* (L.) (Verbenaceae) has been ongoing in South Africa for over 40 years. Despite this, the weed is still not under sufficient control and continues to invade new territories in the country. The biological control programme needs to be bolstered with releases of new and potentially damaging biological control agents.

A promising biological control agent endemic to Central America, *Falconia intermedia* (Distant) (Hemiptera: Miridae), was imported into quarantine from Jamaica in 1994. This agent was released on sites in KwaZulu-Natal and Limpopo provinces of South Africa in 1999. Even though it initially established and damaged *L. camara*, populations died out at most of the release sites. As varietal difference and adverse climate have been cited as the reason for non-establishment and ineffective control in *L. camara* biocontrol programmes worldwide, this study attempts to investigate the role that these two factors play in this weed-herbivore relationship.

Laboratory no-choice trials were conducted to determine the varietal performance of *F. intermedia*, among five Eastern Cape varieties of the weed from East London, Whitney Farm, Heather Glen Farm, Port Alfred and Lyndhurst Farm, and a variety from the Plant Protection Research Institute (PPRI), Pretoria. However, there were differences in performance as the adult mirids performed better on white-pink varieties from Whitney Farm and Heather Glen Farm.

To test varietal preference in field conditions, field releases of *F. intermedia* were also made at East London, Whitney Farm, Heather Glen Farm, Port Alfred and Lyndhurst Farm. Post-release evaluations were conducted monthly for two years (2002 and 2003). The insect established at East London and Whitney Farm, both of which have white-pink varieties. Insect populations quickly died out at the Lyndhurst Farm and Port Alfred sites, which have dark-pink varieties. It is suggested that field conditions may have resulted in poor plant quality and led indirectly to varietal preference, and to non-establishment at these two sites.

With the onset of cooler weather, populations disappeared at Heather Glen Farm. This suggested that *F. intermedia* was suitable for release in more subtropical areas within South Africa where climatic conditions would be suitable throughout the year. The mirid performed well at Whitney Farm, resulting in significant reduction in plant growth parameters such as height and percentage cover, and increasing the cover of other flora growing beneath *L. camara* plants. Finally, ways to improve the efficacy of this agent are considered in an effort towards better control of *L. camara* in South Africa.

Contents

List of Tables

List of Figures

Acknowledgements

I am grateful to my supervisors, Professors Martin Hill and Martin Villet for their guidance, patience and invaluable help throughout this project. I also thank them for going the extra mile and for reading the drafts I submitted, and for ensuring that I learn the necessary lessons I need for research from their wealth of experience.

I thank Dr. Alan Urban and Fritz Heystek from the Plant Protection Research Institute for their support and assistance. I appreciate Alan for getting me on board this project, and Fritz for getting me started and showing me how to do the field work.

I also need to thank the following people: Million Kota for driving me to all the field sites and helping me to measure and record data, despite his fear of snakes; Charles Willemse for assisting me in my field trips, for looking after my plants at the Gardens and Ground Division, Rhodes University, and during the laboratory trials; management and staff at the Garden and Grounds Division for allowing me to grow lantana at their nursery, and for looking after it when I was away; Bronwyn Tweedie from the Graphics Service Unit, Rhodes University for drawing up a map and then editing it numerous time; and Mark Robertson for showing me where major lantana infestations could be found; the owners and managers of the following farms, Whitney Farm, Port Alfred Farm, Lyndhurst Farm, and Heather Glen Farm.

I thank the following family members and friends: Unathi Mbane for her support, encouragement and prayers throughout the project and particularly during the documentation stages; my mother, P.T.A. Heshula, for the support and interest shown during the project; Ngcwengo and Akha, and my sisters, Lizzy and Aluta are also acknowledged for "encouraging me to finish"; and Nkosinathi Mvelo for inspiring me to do more with my life.

I thank and appreciate God for being my inner source of inspiration, without whom I would not have made it through the lowest points of this journey.

This research was funded by the Agricultural Research Council of South Africa and the "Working for Water" Programme, an initiative of the Department of Water Affairs and Forestry (South Africa).

Chapter 1

General Introduction

Preface

This chapter is a review of the origin, biology and distribution of the weed *Lantana camara*. It describes the impacts (economic and environmental) and genetic variation of the weed, and tracks the South African effort to control this weed. Finally, the biological control agent to be released, *Falconia intermedia,* is introduced and the aims of the thesis are discussed.

1.1 Biology and Impact

Lantana camara (L.) *sensu lato* (Verbenaceae), commonly known as lantana, occurs as a native shrub on islands of the West Indies, Central America and South America (Howard 1970). This area is regarded as its generic epicentre, and it is from here that many different varieties of the plant have been introduced to the rest of the world via Europe as an ornamental plant (Stirton 1977). Lantana is a brittle, floriferous, prickly thicket-forming shrub. It is normally 2-4m tall, but it is capable of becoming a liana of up to 15m tall. It grows well in humid areas with consistent rainfall and where soil moisture is readily available, but it can tolerate drought very well by means of defoliation (Swarbrick *et al.* 1995). Its varieties are widely distributed in the tropical, subtropical and warm temperate regions of the world, from the southern USA and the Mediterranean in the north to South Africa and the northern tip of New Zealand in the south. Lantana has become naturalised in more than 50 countries where it has been declared a weed. It was first introduced into South Africa via Cape Town in 1858, and KwaZulu-Natal in 1883 (Stirton 1977) and was declared a weed in 1954. Since introduction, it has naturalised in Limpopo Province, Gauteng, Mpumalanga, KwaZulu-Natal, and the coastal region of the Eastern Cape and the Western Cape. It is among the ten most invasive alien plant species in South Africa. According to Robertson *et al.*'s (2003) prioritisation system for the management of alien species in South Africa, *L. camara* received the highest prioritisation score based on its invasiveness, spatial characteristics, potential impact, potential for control and the conflict of interests arising from controlling it.

Lantana's thicket-forming habits and vigorous growth cause it to be an invader of forests, riverbanks, creek banks, fence lines, veld, and open and semi-open plant communities such as road verges, grasslands and woodlands. It is an aggressive pioneer and a serious invader of disturbed ecosystems, tending to crowd out indigenous flora and suppress natural vegetation, thus reducing the carrying capacity of veld. Such invasions have been reported to increase surface runoff by decreasing the capacity of the soil to absorb heavy rain, leading to flooding. According to Versfeld *et al.* (1998), lantana has invaded a total area of 2 235 395 ha in South Africa and 2 297 ha in the Eastern Cape. Through allelopathic suppression of indigenous plant species, lantana invasions also interrupt regeneration processes (Gentle and Duggin 1997) and reduce the biodiversity of natural ecosystems.

Lantana leaves, stems and fruit contain a number of chemicals toxic to animals, especially two cyclic triterpenes (Everist 1981) that primarily affect ungulates. Photosensitization is the commonest symptom of lantana poisoning in sheep, along with acute and chronic damage to the liver, kidneys and gut, paralysis of the gall bladder, internal haemorrhage and sometimes death within 1-6 days in cattle, horses and sheep (Fourie *et al.* 1987). The expected annual impact of cattle mortalities in South Africa was estimated to be in excess of US$429 293.00 (at an exchange rate of R3.96 to US$1 in 1996) (Kellerman 1996). As lantana usually invades fields and pastures where livestock feed, this exposes the animals to these potentially damaging chemicals and increases the chances of livestock feeding on them. Green lantana fruits also contain toxins and have caused sickness and death in children (Morton 1994).

1.2 Variation within species

The genus *Lantana* L. (Verbenaceae) is native to Central and South America, with a few species occurring in Africa and Asia (Munir 1996). There are four distinct groups recognized within this genus; *Lantana* sections *Calliorheas*, *Sarcolipia*, *Rhytocamara* and *Camara*. The

Lantana section *Camara* is further divided into 3 complexes based on *L. urticifolia*, *L. hirsuta*, and *L. camara* (Sanders 1989, 1998). The latter complex includes the primary weedy complex referred to as *L. camara* L. *sensu lato*. Lantana is part of a synthetic complex that consists of several morphologically similar *Lantana* species (Day and Neser 2000). It was derived through horticultural and natural hybridisation, selection and somatic mutation from a number of similar, and probably closely related, tropical American species (Swarbrick *et al.* 1995).

In South Africa, hybridisation has continued to occur in the field (Spies and Stirton 1982 a, b, c), giving rise to new cultivars unlike the parental ones. Lantana hybridizes easily and there are possibly some 650 hybrid forms worldwide, known as varieties or cultivars (Howard 1969), that are all classified as *L. camara*. According to Spies (1984), *L. camara* locally is still in an active phase of evolution. Even though the species is considered unstable, certain varieties dominate in localised areas and remain relatively stable over time. Lantana cultivars are distinguished either morphologically, by differences in the flowers (size, shape and colour), leaves (size, colour and hairiness), and stems (degree of spinescence) (Smith and Smith 1982), or physiologically, by differences in rates of growth, general vigour, chromosome number, degree of toxicity to livestock, fertility and cytology (Spies and Stirton 1982 a, b; Spies and du Plessis 1987). The morphological and physiological differences among the different cultivars are substantial to the point where each cultivar behaves like, and can be considered, a different weed species (Cilliers and Neser 1991). The cultivars also display differences in vulnerability to insect herbivores and most of the insect species associated with lantana are only able to develop on a few varieties (Radunz 1971; Taylor 1989).

1.3 Control

Chemical control using herbicides is effective but very costly. Such control produces only temporary relief because cleared areas are rapidly re-infested by seedlings and coppice growth from stems and roots (Cilliers and Neser 1991). Mechanical control by means of chopping and sawing, although very efficient, is labour-intensive and expensive. The cost of clearing a high density cover (75%-100%) of *L. camara* in South Africa using herbicides was estimated to be R572 per hectare, and R1000 per hectare using mechanical methods such as felling (Marais *et al.* 2004). There are also additional costs incurred in keeping cleared areas weed-free, which Marais *et al.* (2004) estimated to be R600 per hectare. Controlled low-to-moderate intensity fires appear to reduce invasion by lantana and can be an effective preventative management strategy (Gentle and Duggin 1997). Use of this method of control is however limited by the fact that lantana stands are usually impenetrable, thorny, and in the middle of desired vegetation.

Another control option that has received global attention is biological control using various insect natural enemies. The importation, host-specificity testing and eventual release of an insect agent is time-consuming and expensive though. It takes on average 3-5 years of research to release a natural agent (Broughton 2000), and a variable amount of time for the insect population to establish and grow. In addition, no weed has ever been eradicated by a biological control insect (Harris 1988). Despite these factors, biological control is still one of the best options in the quest to control lantana. Not only can it be environmentally safe, but also the slow action of an insect control agent inhibits the formation of large empty areas where other invaders can establish. Biological control also provides a long-term and cost-effective means of controlling weeds, as agents may be self-sustaining following establishment.

In South Africa, a biological control programme targeting *L. camara* was initiated in 1961/62. Five natural enemies were initially introduced: *Hypena laceratalis* Walker (Lepidoptera: Noctuidae), *Neogalia sunia* Guenèe (Lepidoptera: Noctuidae) and *Salbia haemorrhoidalis* Guenèe (Lepidoptera: Pyralidae); *Ophiomyia lantanae* Froggatt (Diptera: Agromyzidae), and *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae) (Tables 1.1 and 1.2). Other biological control agents were also released on lantana, most notable of these being the two hispine beetles, *Octotoma scabripennis* Guèrin-Mèneville (Coleoptera: Chrysomelidae) and *Uroplata girardi* Pic (Coleoptera: Chrysomelidae), and the leaf-mining fly *Calycomyza lantanae* Frick (Diptera: Agromyzidae). Two of the released insect species, *H. laceratalis* Walker (= *H.*

strigata (F.)) and *O. lantanae* (Table 1.1) are both indigenous to Africa (Pinhey 1975) and were already established in South Africa. *Hypena laceratalis* has since been found to be synonymous to *H. jussalis* Walker, and *O. lantanae* was misidentified as *O. rhodiensis* Spencer, the confusion arising from misidentification by Oosthuizen (1964) during a pre-release survey. *Hypena laceratalis* is widely established and was well known prior to its release. It damages seedlings and new lantana growth, but is limited by larval parasitism by several indigenous parasitoid species. Populations never grow to levels where plants are significantly damaged. *Ophiomyia lantanae* is also widespread and abundant, but has little impact on seed viability due to parasitism. Parasitoid species belonging to four families were found on samples of *O. lantanae*-infested fruits (Cilliers 1987). Even after three releases in 1962, 1968 and 1983, the noctuid moth, *N. sunia,* failed to establish.

The leaf feeding moth, *S. haemorrhoidalis,* had established after release but its range and impact is still unknown (Oosthuizen 1964). The fifth species released, *T. scrupulosa*, is widely established and abundant after a number of releases from various countries but it is not clear whether this has contributed to the success and efficacy of the insect in South Africa (Cilliers and Neser 1991). The insect is considered the most damaging of all the agents released on lantana. It causes periodic defoliation of *L. camara*, and a decrease in seed production. The tingid populations are at their peak in midsummer and consequently cause most of the damage during this time (Cilliers 1987a).

Table 1.1 Status of natural enemies present on *Lantana camara* in South Africa prior to the initiation of the biological control programme in 1961/62 (Baars and Neser 1999).

Order/Family	Natural enemy species	Mode of attack	Status	Limitations
Diptera				
Agromyzidae	*Ophiomya lantanae* (Froggatt)	Fruit miner	Widely established, abundant	Low impact on seed viability, possible high levels of parasitism
Lepidoptera				
Noctuidae	*Hypena laceratalis* (Walker)	Leaf feeder	Widely established, causes considerable damage to seedlings and new growth	Larvae only active late summer and autumn and often parasitized
Pterophoridae	*Lantanophaga pusillidactyla* (Walker)	Flower and seed feeder	Established range unknown; present in low numbers	Low abundance and possible high levels of parasitism
Tortricidae	*Epitonia lantana* (Busck)	Flower peduncle and shoot tip borer	Established range unknown	Unknown
Gracillaridae	*Aristaea onychote* (Meyrick)	Leaf-blister miner	Widely established, but present in low numbers	Possible high levels of parasitism

Two leaf-mining beetles, *Octotoma scabripennis* Guèrin-Mèneville and *Uroplata girardi* Pic, were released in the 1970s in the subtropical areas of the country. Both have established, with *U. girardi* reaching high populations in coastal KwaZulu-Natal. On the other hand, *O. scabripennis* is abundant at inland sites, where populations peak intermittently and in only a few areas (Baars 2002). At their population peaks, both species cause defoliation of *L. camara* stands (Cilliers 1987b). The leaf-mining fly, *C. lantanae* (Frick), has established at a few moist, subtropical areas of the country (Table 1.2). The fly causes characteristic blotch mines on leaves of actively growing plants, seedlings and coppice growth. The impact of *C. lantanae* populations is unknown, but may be reduced by larval parasitism (Baars 2002). Releases of other agents and their present status are summarised in Table 1.2.

Despite the release of a large number of agents, and the establishment of several natural enemies (Cilliers and Neser 1991), the agents have failed to effectively control the spread of the weed and the success of biological control has been limited. This has mainly been attributed to two factors: the genetic diversity of lantana, and climatic conditions in the country of introduction. Natural enemies are presented with numerous physiological and morphological barriers to utilisation, making the interaction between a natural enemy and lantana complex and very difficult to predict. With the form of the weed evolving in its introduced ranges apart from its natural enemies, the agents may be considered as "new" associations according to Hokkanen and Pimental's (1984) classifications, because there is no homeostasis between the plant and the insect. Some natural enemies therefore find insurmountable physiological and morphological obstacles in dealing with the 'new' lantana forms, as each form may have features as distinct as a different species. Cultivars also display differences in susceptibility to insect herbivores, and with most insects being able to develop on only a few specific varieties (Radunz 1971). This presents only a few insects with the opportunity to establish on lantana.

Table 1.2 Present status of other agents on *Lantana camara* in South Africa (Baars and Neser 1999).

Order/Family	Natural enemy	Origin	Main releases	Mode of attack	Status	Damage inflicted
Coleoptera						
Chrysomelidae	*Alagoasa parana* Samuelson	Brazil	1985	Leaf miner	Not established	-
	Octotoma scabripennis Guèrin-Mèneville	Mexico via Hawaii via Australia	1971	Leaf miner	Established in warm moist eastern range of lantana, abundant in localised inland areas	Extensive defoliation localised
	Octotoma championi Baly	Costa Rica via Australia	1978 1995	Leaf miner	Persisted in low numbers for 2 seasons after last last release, unconfirmed establishment	Unknown
	Uroplata girardi Pic	Paraguay via Hawaii via Australia	1974 1983	Leaf miner	Abundant in KZN regions, present in low numbers in warm moist inland lantana range	Extensive coastal defoliation
Diptera						
Agromyzidae	*Calycomyza lantanae* Frick	Trinidad via Australia Florida, USA	1982 1989	Leaf miner	Widely established in low numbers. Heavily parasitized	Unknown
Tephritidae	*Eutreta xanthochaeta* Aldrich	Mexico	1983	Stem galler	Not established	-
Hemiptera						
Tingidae	*Teleonemia scrupulosa* Stål	Mexico via Hawaii via	1961	Flower and leaf sucker	Widely established in large numbers across	Complete defoliation

		Australia via Mauritius Florida, USA	1971 1984 1989		entire lantana range, severe sporadic damage	& abortion of flowers
	Teleonemia elata Drake		1972	Sap sucker	Not established	-
Lepidoptera						
Noctuidae	*Neogalia sunia* Druce	USA	1962	Leaf chewer	Not established	-
Pyralidae	*Salbia haemorrhoidalis* Guenèe	Cuba via Hawaii	1962	Flower and fruit feeder	Widely established in low numbers	Unknown

The diverse climatic conditions in the distribution range of *L. camara* in South Africa have been cited as another reason for the failure of natural enemies to establish on lantana (Neser and Cilliers 1991, Day and Neser 2000). Not only has the weed infested the warm and subtropical coastal regions of the country, such as KwaZulu-Natal, but it is also found through the highveld region (altitude > 1500m) (Henderson 1995) with dry and frosty winters. The plant is capable of surviving adverse conditions, such as drought and very cold winter temperatures, by defoliating. Therefore, natural agents introduced from tropical regions to temperate climes have a small chance of establishing (Sands and Harley 1980). Extremely cold winter temperatures become a barrier for the natural enemies introduced from warm tropical regions and may lead to widespread mortalities in their populations. Furthermore, extensive defoliation during winter may leave leaf-feeding insects with neither food nor shelter, leading to widespread starvation, increased mortality and non-establishment. Lack of over-wintering mechanisms, such as adult or pupal diapause by introduced insects, also contributes to non-establishment (Williams 2003). Insect populations are either wiped out completely, or are greatly reduced during these harsh South African winters. The insect populations become unable to cause any substantial amounts of damage on the lantana because they spend the favourable spring and summer time recovering.

Cilliers and Neser (1991) also proposed other factors that prevent establishment of natural enemies after release. These are (a) herbicidal and mechanical destruction of sites before the insects have had a chance to establish and disperse (e.g. *Octotoma championi* Baly, *Uroplata lantanae* Buzzi and Winder); (b) predation of their eggs, especially by ants (e.g. *Alagoasa parana* Samuelson); (c) unsuitable microhabitats (e.g. *A. parana*), and (d) the numbers released being below a minimum threshold for populations to survive (e.g. *U. lantanae*, *E. xanthochaeta*, *Teleonemia elata* Drake, *Lantanophaga pusillidactyla* (Walker)). According to Broughton (2000), releases of a low number of individuals in an introduction attempt accounted for 23.6% of all cases of failure in lantana programmes worldwide.

1.4 Aims of the research

Lantana camara continues to be one of the most invasive alien species in South Africa despite the large number of natural enemies that have established on it. The biological control agents released onto lantana provide insufficient control to reduce its weedy status. Some success has however been achieved, but was largely not quantified. The relative progress towards successful control is therefore largely uncertain. Since it has been acknowledged that success in controlling this variable weed depends on the release of a suite of natural enemies (Oosthuizen 1964, Cilliers 1987a), a potential biological control agent, *Falconia intermedia* (Distant) (Hemiptera: Miridae) was imported into South Africa for release. After successful host specificity tests in quarantine, this agent was approved for release in South Africa.

Two separate laboratory colonies of *F. intermedia* were collected from Jamaica in 1994 and in Guatemala in 1997. The mirid is endemic to Central America and its adults and nymphs are highly active and mobile, especially when disturbed. The adult is about 2mm long, with a dark brown body and pale legs. The eggs are laid singly or in small groups on the undersurface of leaves. They are translucent pale green and are often covered and cemented to the leaf by a black or dark reddish faecal substance. At high insect densities, eggs may be laid along the invaginated veins on the adaxial leaf surface (Palmer and Cullen 1998). The emergent nymphs are green and wingless. They take about 15-20 days to moult into the adult stage and take a few days to lay eggs. The life span of the insect is about two months and the insect may have up to nine generations in a year (Baars 2002).

The adults and nymphs suck the sap of lantana leaves, mainly on the underside, causing white chlorotic specks visible on the upper leaf surface. This feeding activity can cause affected leaves to desiccate and abscise. Severe feeding damage causes entire shrubs to appear silvery white and leaves to drop. At high densities, insects can lead to defoliation of entire lantana stands (Palmer and Cullen 1998). Feeding starves the leaves of vital resources, and this interferes with the leaves' ability to photosynthesise. This reduces the capacity of lantana to produce new flowers, leaves and shoots. Sustained damage will reduce the aggressive growth of lantana and will enable other indigenous plant species to compete for space and light in the field. This insect was released in South Africa in April 1999 on experimental sites in the KwaZulu-Natal and Limpopo Province (Heystek, pers. comm.). However, the field impact of this new agent has not been quantified. The releases made in December 2001 in the Eastern Cape Province present an opportunity to measure the impact and establishment of the insect in this province.

The weed poses a unique challenge due to its polyploidy nature (Stirton 1977) and extreme variability. The variability of lantana in its naturalised range provides introduced natural enemies with morphological and physiological difficulties in establishment. The effect of several Eastern Cape varieties on the performance of this agent will be tested under laboratory conditions (Chapter 2).

It is assumed that plant fitness is eventually reduced by the leaf-feeding attack of insect herbivores (Van der Meijden 1989). This aspect of the plant-insect herbivore interaction will be explored at sites in the Eastern Cape. The effect that feeding damage has on the growth of the plant, the reproductive output, and therefore potential spread of the weed will be studied (Chapter 3). Recruitment of plants under the canopy could indicate the plant's competitiveness towards other species, once stress of this biological control agent is added.

This research will provide us with the opportunity to compare the performance and impact of the insect herbivore on different Eastern Cape lantana varieties with that of the other provinces where releases have been made. The final chapter (Chapter 4) interprets the results in the context of the South African and global biological control effort against *L. camara* and offers suggestions for the way forward.

Chapter 2

Laboratory performance of *Falconia intermedia* on *Lantana camara* varieties

Abstract

Five Eastern Cape *L. camara* varieties; WP EC1, WP EC2, WP EC3, DP EC1, DP EC2, and a variety from the PPRI, WP O29, were used to determine the performance of *F. intermedia* under laboratory conditions. *Falconia intermedia* found all the varieties suitable for oviposition, with no significant differences recorded among the number of eggs laid, adult survival and number of nymphs. The intensity of damage by *F. intermedia* was generally low to medium at all varieties, with no significant impact on growth parameters such as plant height, length of leading shoots, and reproductive parameters among the varieties. However, the significantly higher number of leaves dropped by the WP EC2 and WP EC3 varieties suggests that the agent may have performed better on these two varieties.

2.1 Introduction

It has been over 100 years since planned attempts at biological control against the weedy form of *L. camara* were first initiated worldwide (Day *et al.* 2003). However, these attempts have met with little success as the weed continues to invade new regions, territories and landscapes. Reports by some authors have cited the morphological variability of *L. camara* as one of the major limiting factors in the success of the biological control programme against this weed (Cilliers and Neser 1991, Day and Neser 2000). The invasive *L. camara* is part of a complex that consists of several morphologically similar species (Chapter 1; Day and Neser 2000). New varieties of this highly variable entity came about through long periods of hybridisation and selection by horticulturists in the 19^{th} century (Stirton 1977). The resultant varieties were unlike the parent species in the native ranges of Central and South America. Records of the parental lantanas and of all the crosses performed were not kept, and therefore the origin of the modern varieties remains unknown (Stirton 1977).

In a paper reviewing the lantana biological control programmes worldwide, Broughton (2000) reported that cultivar preference was cited as the main cause of failure in biological control programmes. The first aspect of the variability problem is the identity of the lantana plant in the native range from which potential agents are collected. The lantana varieties naturalized in other countries are morphologically distinct from the lantana varieties in the native range (Smith and Smith 1982). In most biological control programmes, potential agents are usually collected from the same weed species in its native range (Day *et al.* 2003). In cases such as lantana, where the same species does not exist in the native range, the challenge is to identify the most closely related and most suitable species from which agents can be collected. DNA studies have shown the varieties of *L. camara* in Australia, Vanuatu and Fiji to be closest to *L. urticifolia* (Miller) in the naturalized range (Scott 1998), but comparable studies have not been published regarding the South African varieties. Even when a suitable biological control species has been found, there is still the possibility that the agents will not establish due to incompatibility with the varieties in the field. However, this is usually resolved by pre-release multivariate host-specificity tests in quarantine.

A second aspect of the problem is the varietal differences of lantana in the naturalised regions. There are more than fifty *L. camara* varieties in South Africa (Wells and Stirton 1988), with 17 in KwaZulu-Natal alone (Stirton and Erasmus 1990), and 29 varieties in Australia (Smith and Smith 1992). With the weed's continued hybridisation in the field in South Africa (Spies and Stirton 1982a, b, c), the variety numbers may have increased. Lantana varieties exhibit differences in their flower colour, spininess, leaf shape and susceptibility to insect attack (Chapter 1; Howard 1970; Smith and Smith 1982; Munir 1996). Furthermore, differences have also been reported in the cytology and genetic composition of different varieties (Spies and Stirton 1982a, b; Spies and du Plessis 1987). Each variety exhibits such different morphological, chemical and physiological features, that each variety may be considered a separate species (Cilliers and Neser 1991).

Due to this variability, biological control agents have been reported to display differences in performance and preference on the naturalized varieties. Cilliers and Neser (1991) found *Hypena strigata*, *Octotoma scabripennis*, *Calycomyza lantanae* and *Uroplata girardi* to all show a preference for pink-flowering varieties. Haseler (1966) reported that *Neogalia sunia* showed preference for white- and pink-flowering varieties in Australia. *Teleonemia scrupulosa* was also found to not perform well on pink varieties in Australia (Harley 1973), and varietal preference was implicated in the non-establishment of this agent in Yap (Muniappan 1989; Schreiner 1989). On the other hand, Broughton (1999) found that five leaf-feeding insect species, including *T. scrupulosa*, *C. lantanae*, *U. girardi* and *O. scabripennis*, showed no variety preferences in field studies conducted in southeast Queensland. Neser and Cilliers (1989) found that among these, *T. scrupulosa* exhibited varietal preference in South Africa. Laboratory trials also revealed clear varietal preference in *F. intermedia*, with populations dying out on less preferred varieties (Urban and Simelane 1999). However, after conducting varietal preference trials under laboratory conditions, Baars (2002) suggested that the role of varietal preference in failure of biological control was overestimated. Even though there are sufficient quantitative studies to support the varietal preference argument, it is also quiet clear that a number of other reports were arrived at by personal observation. This suggests that more studies should be conducted to give direct indications of possible agent-host interaction.

Insect feeding can have an injurious effect on the host plant when an agent has been released on an appropriate host. In Guam, leaf-feeding insects such as *O. scabripennis*, *U. girardi*, and *T. scrupulosa* are known to injure lantana to some extent, increasing defoliation by up to 70% (Broughton 2000) and decreasing fruit production by as much as 70.1% compared to control plants (Muniappan *et al.* 1996). The leaf-feeding noctuid moth, *Hypena laceratalis* (Walker), has been reported to cause severe seasonal damage to lantana in Queensland, Australia. Such results have not been repeated in other countries where releases were made, and according to Day *et al.* (2003) this is partly due to poor performance on some lantana varieties.

The most successful biological control agents in the lantana programmes have been leaf-feeders (Broughton 2000). The surface area of the leaf and growth rate are reduced by leaf-feeding activity (Winder 1980). This may reduce the competitive ability and storage reserves of the plant. It is assumed that plants have a limited budget against insect attack, because other functions such as growth, maintenance and reproduction cannot be stopped completely to allow for the continuous allocation of reserves for compensatory measures (Van der Meijden 1989). Therefore, sustained attack by leaf-feeding insects would be expected to eventually reduce the fitness of lantana.

Even though some of the above agents have damaged lantana in the field, this can be difficult to show. In this chapter, the effect of selected *L. camara* varieties on the preference and performance of *F. intermedia* in laboratory conditions is tested. Although such studies can not demonstrate *per se* the effect a biological control agent may have on plant population dynamics, they can give an indication of the effect an agent might have on the host plant itself (Crawley 1989c), and vice versa. The conducted studies will also be important in identifying the preferred Eastern Cape lantana varieties for *F. intermedia* to enable more informed and effective releases in future.

2.2 Materials and Methods

2.2.1 Laboratory performance and varietal preference of *Falconia intermedia*

Lantana camara cuttings were collected from five Eastern Cape experimental sites (East London, Whitney Farm, Port Alfred, Lyndhurst Farm, Heather Glen Farm) (Fig. 3.1) and the WP 029 variety from Plant Protection Research Institute (PPRI) for propagation in a nursery (Table 2.1). The five Eastern Cape experimental sites were selected to represent a climatic range of the province and to include different but common lantana varieties found within the province (Table 3.1). The sites were used in the field trials for post-release evaluations of the mirid (chapter 3), and thus offered and opportunity to compare the laboratory and field performance of *F. intermedia* on *L. camara*. Shoots of about

15cm were cut from the parent plants and all leaf pairs were removed except the apical pair. The shoots were wrapped in moist paper for transportation back to the nursery. The cuttings were dipped into a root growth hormone (Dip and Grow®) and planted in river sand to encourage root growth. Cuttings were watered as necessary. After 4-6 weeks the cuttings were transplanted into individual pots in a standard potting mixture and allowed to grow to about one metre tall.

Falconia intermedia adults were collected from Whitney Farm, where insects had established following releases in December 2001. The culture was maintained on the WP029 variety from PPRI under laboratory conditions with a 14-hour photoperiod. The reproductive performance of the mirid on this variety was good in studies conducted by Baars (2002). Experiments were conducted in an insectary where the temperature varied 18°C at night and 33°C in the day. Light was provided by grow lux lighting with a day length of 14 hours.

Nine plants from each of the six varieties (five naturalised Eastern Cape varieties and WP 029 (PPRI)) were selected for this trial. These were grouped into three treatments for each variety, with three replicates in each treatment. For treatment 1 the plants were removed from the pots and dried at 70°C for 48 hours in an oven. After this the above-ground (flower, seed and leaf) and below-ground (root) dry weight was recorded as the average initial dry biomass. This information was used as a benchmark for comparison with the final above- and below-ground dry weights of treatments 2 and 3. Plants in treatment 2 and 3 were placed in individual cages. Treatment 2 was a control that was left with no *F. intermedia* adults, while 0.5 adults per leaf pair were released on each plant in the last treatment.

Initial plant height and the number of main and side branches were counted on each plant in each treatment. The number of flowers, seeds and leaf pairs at the beginning of the experiment was recorded for each plant. Trials were conducted for 8 weeks, after which final measurements of the plant height, leading shoot length (length of longest continuous shoot from base of plant) and numbers of side branches and the number of seeds and flowers, were recorded on the plants of treatments 2 and 3. The number of damaged leaves per plant was recorded, and was also converted to a proportion based on the total number of leaves remaining. The mean damage on the damaged leaves was then determined by adding the individual damage of each leaf and then dividing this by the number of damaged leaves. Damage was scored by multiplying the leaf area damaged (0-4) by the intensity of the damage (0-3) (Table 2.2). The number of dropped leaves and adult survival were recorded for each plant and the number of eggs produced was recorded as a measure of the fertility of the insects on each variety's treatment. Plants in treatments 2 and 3 were dried in a drying oven at 70°C for 48 hours and the above- and below-ground biomass weighed and recorded for each variety.

Due to the small number of replicates per treatment used in this experiment, the more robust Kruskal Wallis ANOVA was used to analyse endpoint data at the 5% level of significance for each variety. The interactions between the means of the variables were separated by multiple comparison rank tests on the Statistica 6.0® programme.

Table 2.1 Distinguishing characteristics and the original locations of *Lantana camara* varieties used during laboratory trials.

L. camara variety	Distinguishing morphological features	Flower colour	Original Site location	Grid reference
WP EC1	Leaves large, broad, dark, hairy; shoots hairy and spiny; main stem spiny	White Pink	East London	33°00'23"S 27°54'47"E
WP EC2	Leaves large, broad, dark, hairy; Shoots spiny; main stem spiny	White Pink	Whitney Farm	33°40'43"S 26°35'49"E
WP EC3	Leaves large, broad, dark, hairy; shoots hairy and spiny; main stem spiny	White Pink	Heather Glen Farm	33°19'28"S 26°47'31"E
DP EC1	Leaves small, tough, hairy; shoots hairy and spiny; main stem with few spines	Dark Pink	Lyndhurst Farm	33°27'11"S 26°53'10"E
DP EC2	Leaves small, tough, hairy, shoots spiny; main stem with few spines	Dark Pink	Port Alfred	33°36'16"S 26°52'16"E
WP 029 (PPRI)	Leaves large, broad, dark, hairy; shoots spiny; main stem spiny	White Pink	Hazyview, Mpumalanga	25°08'10"S 30°00'09"E

Table 2.2 Definitions of *Falconia intermedia* leaf damage ratings.

Area Damaged	Area Rating
0%	0
1-25%	1
26-50%	2
51-80%	3
>81%	4
Intensity of feeding damage	Intensity Rating
None	0
Low (few, uneven speckles in affected area)	1
Medium (uniform white speckling, with green spots among yellow/white in affected area)	2
High (white speckling merging, appear almost uniform white/yellow in affected area)	3
Final Damage Rating = Area Rating x Intensity Rating (Range: 0-12)	

2.3 Results

2.3.1. *Falconia intermedia* population parameters

2.3.1.1 Number of *Falconia intermedia* adults per leaf pair

At the end of eight weeks the test treatment on the Lyndhurst Farm (DP EC1) variety had the greatest number of *F. intermedia* adults per leaf pair of all the varieties, with a mean of 0.4 adults per leaf pair (Table 2.3). The Whitney Farm (WP EC2) and Heather Glen Farm (WP EC3) varieties also yielded high numbers of adults, each with a mean of 0.3 adults per leaf pair. Despite the insect culture being maintained on the PPRI (WP 029) variety, this variety had the lowest number of *F. intermedia* adults per leaf pair. There were however no statistically significant differences among any of the sites ($H(5, N=36) = 1.023104$, $p = 0.96$).

2.3.1.2 Number of *Falconia intermedia* nymphs per leaf pair

A trend similar to the one for the numbers of adults was observed for the numbers of nymphs. The test treatment plants of the DP EC1 variety from Lyndhurst Farm had the greatest number of nymphs per leaf pair, with 0.1 (Table 2.3). The other varieties yielded lower numbers of nymphs per leaf pair, with the PPRI (WP 029) variety recording no nymphs at all. In spite of all this, the differences in the number of *F. intermedia* nymphs recorded were not statistically significant between the test treatments of the varieties tested ($H(5, N=18) = 4.334840$ $p = 0.50$).

2.3.1.3 Number of eggs per leaf pair laid by *Falconia intermedia*

Falconia intermedia females laid the greatest numbers of eggs per leaf pair on the WP 029 variety. A mean of 6.6 eggs per leaf pair was laid on this variety (Table 2.3), indicating that it was suitable for *F. intermedia* oviposition despite the low number of adults and nymphs it recorded. The WP EC1 (East London) variety had 5.1 eggs per leaf pair, while the Whitney Farm (WP EC2) and Heather Glen (WP EC3) varieties had the lowest number of eggs per leaf pair laid in comparison with all the other varieties tested ($H(5, N=18) = 5.795455$, $p = 0.327$).

Table 2.3 Means (and standard errors) of *Falconia intermedia* population parameters for the test treatments of the five Eastern Cape sites *Lantana camara* varieties for the laboratory trials. Means in the same column followed by the same letter are not significantly different ($p > 0.05$, Kruskal-Wallis ANOVA). Means separated by multiple comparison rank tests.

Source site	Variety	*n*	Adults per leaf pair	Nymphs per leaf pair	Number of eggs per leaf pair
East London	WP EC1	3	0.3 (0.09) *a*	0.04 (0.03) *a*	5.1 (3.33) *a*
Heather Glen	WP EC3	3	0.3 (0.10) *a*	0.06 (0.03) *a*	2.4 (1.59) *a*
Lyndhurst	DP EC1	3	0.4 (0.07) *a*	0.13 (0.11) *a*	4.6 (2.79) *a*
Port Alfred	DP EC2	3	0.3 (0.10) *a*	0.02 (0.01) *a*	2.3 (1.34) *a*
PPRI	WP 029	3	0.3 (0.11) *a*	0 (0.00) *a*	6.6 (1.07) *a*
Whitney Farm	WP EC2	3	0.3 (0.11) *a*	0.03 (0.03) *a*	1.7 (1.52) *a*

2.3.2 Leaf damage

2.3.2.1 Percentage of *Lantana camara* leaves damaged by *Falconia intermedia* feeding

The Lyndhurst Farm (DP EC1) variety had the greatest proportion of leaves damaged by the mirid (Table 2.4) in its test treatment. This was expected because this variety had the highest number of adults and nymphs among the varieties. The Whitney Farm (WP EC2) and Heather Glen Farm (WP EC3) varieties showed the lowest proportions of leaves damaged, around 25% each. These two results are misleading though, as these two varieties lost a considerable amount of leaves due to heavy damage by *F. intermedia* (Table 2.6, pers. obs.). In reality, the PPRI (WP 029) variety had the lowest proportion of damaged leaves $H(5, N=18) = 2.507427$, $p = 0.77$)

2.3.2.2 *Falconia intermedia* feeding damage on *Lantana camara*

There was no statistically significant difference ($H(5, N=18) = 2.742314$, $p = 0.74$) in the intensity of the feeding damage between the test treatments of all the varieties (Table 2.4). This measurement gives only the feeding damage of the mirid-affected leaves, and among these the Lyndhurst Farm (DP EC1) variety experienced marginally higher mean damage intensity than the Port Alfred (DP EC2), East London (WP EC1) and PPRI (WP 029) varieties. This means that most of the leaves on these four varieties were affected on average with a low to moderate feeding intensity, and that the area of the leaves damaged by *F. intermedia* was on average between 26% and 100% (Table 2.2).

2.3.3 Impact of *Falconia intermedia* on *Lantana camara* growth

2.3.3.1 Number of Leaves

There were no statistically significant differences in the number of leaves remaining at week 8 in the treatments of the various varieties (Table 2.5). The two varieties that dropped the most leaves of their test treatments; Whitney Farm (WP EC2) with a mean loss of 257 leaves and Heather Glen Farm (WP EC3) with a mean of loss 185 leaves (Table 2.6) after week 8, recorded a mean total number of leaves on their test treatments that was somewhat lower than that at their control treatments, even though this was not

Table 2.4 Means (and standard errors) of *Falconia intermedia* feeding damage intensity and proportion of leaves damaged on six *Lantana camara* varieties in laboratory trials conducted over 8 weeks. Means followed by NS indicate no significant difference between a variety's treatment ($p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ (Kruskal-Wallis ANOVA).

Source Site	Variety	n	Feeding damage	Percentage leaves damaged
East London	WP EC1	3	4.4 (4.36) *a*	35.5 (5.01) *a*
Heather Glen	WP EC3	3	3.6 (5.11) *a*	25.3 (18.31) *a*
Lyndhurst	DP EC1	3	4.9 (4.24) *a*	53.6 (23.08) *a*
Port Alfred	DP EC2	3	4.8 (2.99) *a*	31.8 (9.41) *a*
PPRI	WP 029	3	4.4 (5.37) *a*	29.4 (4.12) *a*
Whitney Farm	WP EC2	3	1.8 (6.44) *a*	25.0 (25.04) *a*

significantly so for each of the two varieties (WP EC2, $H(1, N=12) = 1.256410$ $p = 0.26$; WP EC3, $H(1, N=12) = 2.836842$ $p = 0.092$). Three varieties, East London (WP EC1) ($H(1, N=12) = .0256410$ $p = 0.873$), Lyndhurst (DP EC1) ($H(1, N=12) = 0.4102564$, $p = 0.522$) and PPRI (WP 029) ($H(1, N=12) = 0.4102564$, $p = 0.522$), recorded almost the same number of remaining leaves in their test and control treatments, with no statistically significant differences here either. However, among these, the test treatment of the Lyndhurst (DP EC1) variety gained a mean 115.6 leaves after week 8 compared to a loss of 7.3 leaves for its control treatment, while the other two varieties gained or lost a similar amount of leaves on their treatments (Table 2.6).

2.3.3.2 Plant Height

Plant height was not greatly affected by the feeding of *F. intermedia* (Table 2.5). The mean plant heights at all of the varieties were not significantly different between their treatments. Even the two varieties where the mirid had the greatest success and impact on lantana, Whitney Farm (WP EC2) (H (1, N= 12) = 2.084211, p = 0.15) and Heather Glen Farm (WP EC3) (H (1, N= 12) = 3.402924, p = 0.07), had little difference in their test and control treatments.

2.3.3.3 Length of Leading Shoots

The lengths of the chosen leading shoots showed a result similar to those of plant height (Table 2.5). Whitney Farm (WP EC2) (H (1, N= 12, p = 0.29) and Heather Glen Farm (WP EC3) (H (1, N= 12) = 3.705263, p = 0.05) varieties both showed no statistically significant differences between their respective test and control treatments. All the other varieties had the same result between their treatments.

2.3.3.4 Number of Side Shoots

The Heather Glen Farm (WP EC3) (H (1, N= 12) = 4.689474, p = 0.03), variety showed a significantly lower number of side shoots in the test treatment than in the control treatment (Table 2.5). This variety was seriously damaged by the feeding of the mirid. The other variety with some mirid success, Whitney Farm (WP EC2) (H (1, N= 12) = 0.0065711, p = 0.94), showed no significant difference between its test and control treatments. The other four varieties also showed no significant differences in the number of side shoots growing in their respective test and control treatments.

2.3.3.4 Above-ground Biomass

There were no statistically significant differences in the masses of the three treatments in all the different sites (Fig. 2.1). Only in the Whitney Farm (WP EC2) (H (2, N= 9) = 0.62222, p = 0.73) and Heather Glen Farm (WP EC3) (H (2, N= 9) = 1.4222, p = 0.49) varieties do the test treatment have a lower mass than the benchmark (C_0) and control (C) treatments. Even though this difference is not significant, it does indicate that the feeding

Table 2.5 Means (and standard errors) of *Lantana camara* plant growth parameters in laboratory trials conducted over 8 weeks. Means followed NS indicate no significantly difference between a variety's treatments ($p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ (Kruskal-Wallis ANOVA). T= test treatment; C = control treatment. Means separated by multiple comparison rank tests.

Source Site	Variety	n	T/C	Plant Height (cm)	Leading Shoots (cm)	No. of Side Shoots	No. of Leaves
East London	WP EC1	3	T	65.7 (4.36)	88.8 (2.39)	13.8 (2.13)	241.5 (52.04)
		3	C	79.8 (6.02) *NS*	111.7 (12.28) *NS*	16.2 (1.96) *NS*	235.8 (57.29) *NS*
Heather Glen	WP EC3	3	T	61.0 (5.11)	66.2 (7.04)	9.3 (1.56)	190.6 (69.89)
		3	C	73.2 (2.36) *NS*	89.2 (4.99) *NS*	14.8 (1.19) *	307.5 (47.79) *NS*
Lyndhurst Farm	DP EC1	3	T	73.0 (4.24)	68.8 (7.23)	13.0 (2.32)	277.2 (44.92)
		3	C	69.3 (7.66) *NS*	92.2 (7.45) *NS*	13.3 (0.62) *NS*	243.3 (43.12) *NS*
Port Alfred	DP EC2	3	T	72.3 (2.99)	88.7 (4.68)	16.5 (1.38)	203.2 (33.27)
		3	C	66.0 (5.05) *NS*	74.2 (7.37) *NS*	12.8 (2.02) *NS*	153.7 (24.04) *NS*
PPRI	WP 029	3	T	60.0 (5.36)	90.7 (8.12)	14.5 (1.12)	109.3 (20.89)
		3	C	73.2 (3.16) *NS*	87.7 (5.45) *NS*	15.8 (1.42) *NS*	104.5 (12.64) *NS*
Whitney Farm	WP EC2	3	T	66.3 (6.44)	79.8 (9.47)	16.7 (1.23)	220.8 (68.99)
		3	C	77.7 (3.95) *NS*	88.3 (4.97) *NS*	16.7 (1.43) *NS*	352.5 (74.17) *NS*

has had some impact on these varieties, and may have continued to do so with more and an increase in damage.

2.3.3.5 Below-ground Biomass

Once again the two varieties Whitney Farm (WP EC3) ($H(2, N=9) = 1.06667$, $p = 0.58$) and Heather Glen Farm (WP EC2) ($H(2, N = 9) = 4.3025$, $p = 0.12$) , and Port Alfred (DP EC2) ($H(2, N = 9) = 2.48889$, $p = 0.28$), had lower masses among their three treatments (Fig. 2.2). However, there were no statistically significant differences in masses in any of the treatments in any variety.

2.3.4 Impact of *Falconia intermedia* on reproductive ability of *Lantana camara*

2.3.4.1 Number of Flowers

The feeding damage and activity of the mirid had a negligible effect on all of the varieties tested. There were no statistically significant differences in the number of flowers produced by the test and control treatments of each variety (Table 2.7). Most of the plants had no flowers towards the end of the 8-week trial. This was due to seasonal effects, as the last two weeks of the trial were conducted in May 2004.

2.4.3.2 Number of Seeds

A trend similar to the one observed for flowers was observed for seeds. The number of seeds showed no statistically significant differences between any of the test and control treatments of the six varieties (Table 2.7). All of the plants recorded no seeds after 8 weeks, and this may be due to the relationship between the production of flowers and the production of seeds.

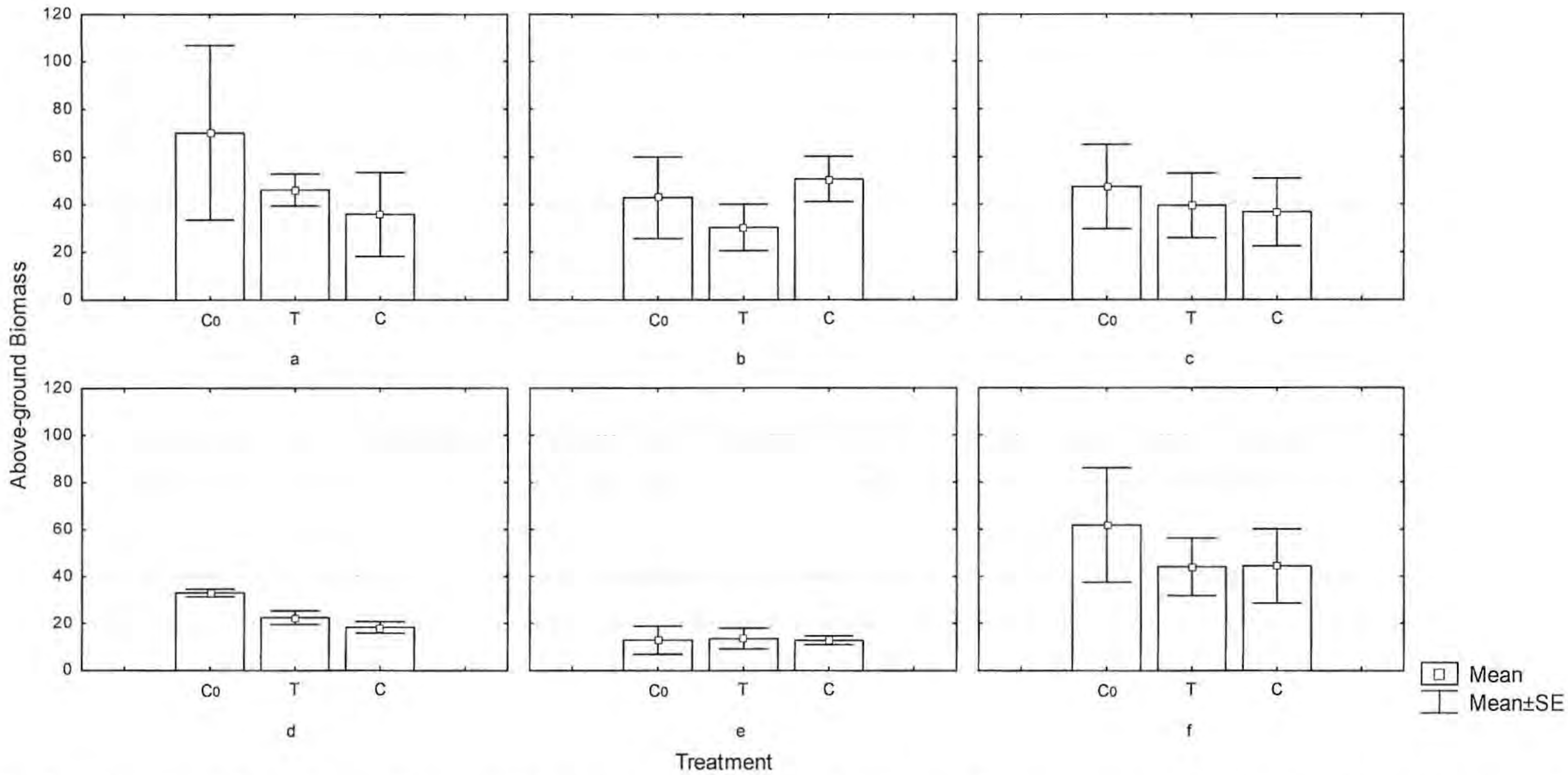

Fig. 2.1 Mean plots of above-ground biomass of the three treatments for the six different *Lantana camara* varieties. Vertical bars denote ± SE. Means followed by the same letter are not significantly different ($p > 0.05$, Kruskal-Wallis ANOVA). Italic letters indicate differences between treatments within one variety, and not between varieties. a = East London (WP EC1), b = Heather Glen (WP EC3), c = Lyndhurst (DP EC1), d = Port Alfred (DP EC2), e = PPRI (WP 029), f = Whitney Farm (WP EC2).

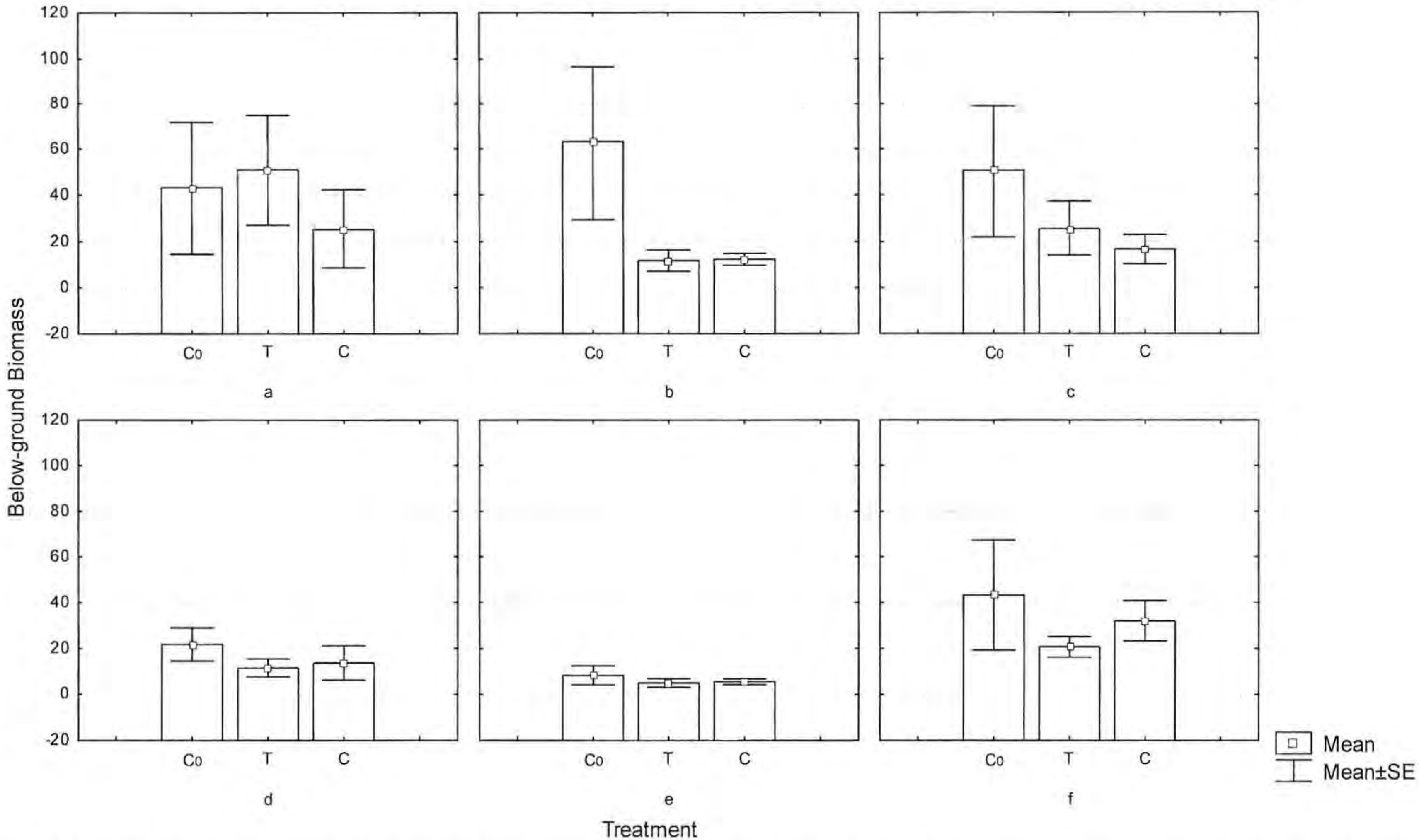

Fig. 2.2 Below-ground biomass mean plots of the three treatments for the six different *Lantana camara* varieties (Vertical bars denote ± SE). Means followed by the same letter are not significantly different ($p > 0.05$, Kruskal-Wallis ANOVA). Italic letters only indicate differences between treatments within one variety, and not between varieties. a = East London (WP EC1), b = Heather Glen (WP EC3), c = Lyndhurst (DP EC1), d = Port Alfred (DP EC2), e = PPRI (WP 029), f = Whitney Farm (WP EC2).

Table 2.6 Mean numbers of leaves (and standard errors) gained (+) or dropped (-) on the test and control treatments of the *Lantana camara* varieties after 8 weeks. Means followed NS indicate no significantly difference between a variety's treatments ($p > 0.05$), * = $p < 0.05$ (Kruskal-Wallis ANOVA). T = test treatment; C = control treatment. Means separated by multiple comparison rank tests.

Source Site	Variety	n	T/C	Gained/Dropped Leaves
East London	WP EC1	3	T	-27.7 (75.17)
		3	C	-43.7 (61.41) *
Heather Glen Farm	WP EC3	3	T	-185.3 (126.31)
		3	C	+44.3 (14.62) *
Lyndhurst Farm	DP EC1	3	T	+115.7 (16.38)
		3	C	-7.3 (51.09) *
Port Alfred	DP EC2	3	T	+68.3 (14.19)
		3	C	+49.3 (16.95) *NS*
PPRI	WP029	3	T	+55.3 (12.19)
		3	C	+35.7 (29.53) *NS*
Whitney Farm	WP EC2	3	T	-257.0 (120.70)
		3	C	+38.3 (55.44) *NS*

Table 2.7 Means (and standard errors) of *Lantana camara* reproductive parameters in laboratory trials conducted over 8 weeks (Mean ± SE). Means followed NS are not significantly different (Kruskal-Wallis ANOVA). T = test treatment, C = control treatment. Means separated by multiple comparison rank test.

Source Site	Variety	n	T/C	Flowers	Seeds
East London	WP EC1	3	T	0.3 (0.33)	1.3 (0.84)
		3	C	1.8 (0.98) *NS*	8.2 (3.67) *NS*
Heather Glen	WP EC3	3	T	1.2 (0.75)	6.3 (4.31)
		3	C	0.0 (0.0) *NS*	30.3(15.12) *NS*
Lyndhurst Farm	DP EC1	3	T	2.0 (1.48)	3.3 (3.33)
		3	C	0.2 (0.17) *NS*	0.8 (0.83) *NS*
Port Alfred	DP EC2	3	T	1.2 (0.83)	8.0 (3.82)
		3	C	0.5 (0.50) *NS*	3.8 (2.81) *NS*
PPRI	WP 029	3	T	0.7 (0.67)	1.3 (1.33)
		3	C	0.3 (0.21) *NS*	0.0 (0.00) *NS*
Whitney Farm	WP EC2	3	T	2.0 (1.18)	9.8 (6.51)
		3	C	0.8 (0.54) *NS*	4.2 (3.77) *NS*

2.4 Discussion

2.4.1 *Falconia intermedia* population parameters

There was sufficient oviposition in all of the varieties tested in these no-choice trials to suggest that *F. intermedia* found all the varieties suitable to various degrees for oviposition. The PPRI (WP029) and East London (WPEC1) varieties seem to be the most preferred varieties for *F. intermedia* oviposition under laboratory conditions among the varieties tested, albeit statistically non-significantly in relation to the other varieties. This result was to be expected for the WP029 variety as the mirid culture was maintained on this variety before the experiment, and would thus have been conditioned by feeding on this variety. The result also concurred with results obtained by Baars (2002) in *F. intermedia* pre-release evaluation trials, where the mirid demonstrated good reproductive performance on this variety. Although the similar distinguishing morphological features of these two varieties may have had a positive effect on this result, this is difficult to show (Table 2.1) as the factors influencing host acceptability are yet unknown.

Based on the number of adult and nymphs surviving and the number of eggs laid on these two varieties compared to other varieties, it can also be inferred that they probably had slightly higher eggs-per-female ratios than other varieties, indicating that they are probably more suitable for oviposition relative to the other varieties. Care should be taken in interpreting the results for the Whitney Farm (WPEC2) and Heather Glen (WPEC3) varieties as suggesting that they are least preferred among the tested varieties, in particular due to the low number of eggs recorded on them. The high number of leaves dropped by the Whitney Farm (WP EC2) and Heather Glen Farm (WP EC3) varieties may have negatively affected the number of eggs, resulting in wrong conclusions. The oviposition results showed that the five Eastern Cape varieties form part of the mirid's fundamental host range.

The number of individuals surviving was generally low on all varieties, including the WP029 variety on which the *F. intermedia* culture was maintained. It was observed after release that a number of adults died within the first few days on a number of the varieties. This can however not be explained, but the fact that the mirid culture was reared on one biotype of lantana and then released onto another may have contributed to mortality on the non-WP029 varieties. The life cycle of *F. intermedia* may also have had an effect on the low number of adults surviving after week 8, as adults live for about 2 months in laboratory conditions, the duration of the experiment (Baars 2002). Therefore the end of the life cycle for some individuals might have overlapped with the end of the experiment, or may have even come sooner, as the adults were not all newly emerged at the start of the experiment.

The number of leaves dropped by the Whitney Farm (WP EC2) and Heather Glen Farm (WP EC3) varieties probably affected the number of adults and nymphs recorded. Leaf drop would not only have resulted in a biased count of the number of eggs, because they would fall with the dropping leaves, but may have resulted in nymphal mortalities. Some nymphs dropping with the leaves were not able to make their way up the plants again (pers. obs.). Adults on these varieties may also have been faced with food shortage and shortage of oviposition sites as leaves were dropped. Therefore the level to which the mirid performed on these varieties for oviposition as well as adult and nymphal survival on these two varieties needs further testing.

2.4.2 Varietal susceptibility to *Falconia intermedia* damage

Feeding damage to the lantana varieties ranged from low to medium in intensity. This was due to low numbers of individuals present at the end of the trial, leading to much lower insect per leaf-pair ratios than the 4 leaves/adult at the start, essentially meaning that adult and nymphal mortalities resulted in less feeding pressure. Even on the Lyndhurst (DP EC1) variety, with the highest number of individuals at week 8, the mirid damage was not high nor was the impact on the variety's growth great. With sufficient time the individuals may have had a more significant impact.

The Heather Glen Farm (WP EC3) variety dropped significantly more leaves at its test than control treatment (H (H (1, N= 6) =3.857143 p =.049), even though the leaves counted at this variety at the end of the experiment yielded no significant differences between the treatments. This may explain the low damage intensity for this variety as damage measurements were taken from remaining leaves. The high number of leaves dropped may be an indication that in these two varieties adequate stress was placed on the plant due by feeding damage, and this may have resulted in greater number of leaves lost. An increased number of replicates as well as an increase in trial time may have helped in further clarifying the above issues. The poor light conditions in the laboratory may have negatively influenced the overall growth of the lantana, resulting in the odd trends observed in the Lyndhurst Farm above-ground biomass.

The small effect of feeding damage on the plant growth variables such as plant height and length of leading shoots was expected due to low damage and few individual mirids surviving on the varieties. Seasonal conditions played a considerable role in the reproductive capabilities of the *L. camara* varieties. Very few flowers and no seeds were recorded in all treatments. This was most likely because the experiment were conducted in late autumn and early winter of 2004 at an inland site (Grahamstown). It is also possible that light conditions played a role in the lack of flowers observed in all the varieties. There was no indication of reproductive compensation in any of the varieties. Neither was there any compensatory growth in response to feeding damage.

2.4.3 Conclusion

The results suggest that *F. intermedia* has a good chance of establishment in field conditions as the tested varieties accepted could be regarded as adequate hosts. Indications from the Heather Glen (WPEC3) and Whitney Farm (WPEC2) varieties are that the mirid will have an impact especially on the varieties. With time this may be meaningful in the overall growth of the plant, as the leaves are a resource-producing part of the plant. The performance of the mirid may vary from variety to variety, with the mirid most likely to have better performance on the common white pink varieties in the Eastern Cape. However these results must be interpreted and accepted with some measure of caution. The laboratory host range observed in laboratory conditions is often not realised in field conditions (Harris and McEvoy 1995, Marohasy 1998, Hill *et al.* 2000).

Chapter 3

Field impact assessment of *Falconia intermedia* on *Lantana camara* at five sites in the Eastern Cape Province

Abstract

This chapter reports on the results of *F. intermedia* releases made on *L. camara* varieties at five sites, two coastal and three inland, in the Eastern Cape in December 2001. Post-release evaluations were conducted over two years with various *F. intermedia* reproductive and growth parameters, *L. camara* reproductive and growth parameters, floral growth underneath the *L. camara*, and various climatic indicators measured to determine the establishment and impact of *F. intermedia* on *L. camara*. *Falconia intermedia* established only at the two climatically suitable sites, East London and Whitney Farm, and failed to establish due to adverse climatic conditions at one site, Heather Glen Farm. It is suggested that the lack of establishment at the other two sites, Port Alfred and Lyndhurst Farm, was due to inferior soil and plant quality, resulting in this variety being unsuitable for *F. intermedia* reproduction and survival. Populations at the East London site persisted in low numbers due to cooler temperatures in 2003, and no major impact was made on *L. camara*. At the Whitney Farm site the insect feeding activity resulted in a significantly lower *L. camara* cover, and significantly greater cover of grasses, herbaceous plants and creepers, demonstrating the effectiveness of this biocontrol agent.

3.1 Introduction

Even though a number of studies have cited varietal preference as an important limiting factor in the establishment and effectiveness of biological control agents, it is generally accepted that climate is one of the most important factor in the establishment, distribution and effectiveness of agents (Day and Neser 2000, Day *et al.* 2003). An example of this is the establishment of *Leptobrysa decora* Drake (Hemiptera: Tingidae) and the leaf-mining beetle *Uroplata fulvopustala* Baly (Coleoptera: Chrysomelidae) at only a few tropical release sites in northern

Queensland despite numerous releases in more temperate localities. Another leaf-miner, *Octotoma championi* Baly, shown to have a preference for shaded conditions and cooler climates (Taylor 1989), only established in temperate regions of New South Wales and a few sites in the cooler and protected areas of the tablelands of north Queensland (Day *et al.* 2003). In South Africa, *O. scabripennis* was reported to be restricted to the moist subtropical coastal areas of the country, preferring these to the drier inland areas (Cilliers and Neser 1991, Baars 2002).

Climate can have numerous effects on biological control agents, the target weed and the insect-plant host interaction. Temperature and photoperiod can affect the host locating behaviour of adults (Papaj and Rausher 1983), while low temperatures may slow vital physiological processes, reduce the potential rate of population growth and induce diapause in some species. Low temperatures can also lead to inactivity, making an insect more vulnerable to predation. Therefore agents released in ranges that are climatically very different from their native ranges are unlikely to establish (Sands and Harley 1980).

Adverse climate may also act on plant characteristics, making an otherwise suitable plant unsuitable. Variation in climatic conditions causes differences in plant resources and thus affects the insect's survival, fecundity and development rate (Gassman 1996). For example the cold and dry winters of South Africa have been reported to increase biological control agents' mortalities over this period (Harley *et al.* 1979, Cilliers and Neser 1991). This is especially true for leaf-feeding insects whose populations tend to follow seasonal variations that are directly linked to the condition and health of the plant. As plants completely or partially defoliate over winter, insect mortalities increase due a lack of food resources. This creates a lag period in spring where leaf-feeding insects have to recover in numbers, and where lantana can also recover. Leaf-feeding insects are therefore more likely to be effective as control agents in moist and warm sites where lantana retains leaves throughout the year.

Despite the above facts, leaf-feeding insects have been the most successful in controlling lantana (Broughton 2000). In South Africa there is therefore a need to import agents that will increase the pressure on the resource-producing part of the plant, the leaves (Baars and Neser 1999), due to the lack of success in the biocontrol programme thus far. For this purpose, Baars and Neser (1999) suggest that agents having the biological ability to attain high populations very quickly and damage lantana extensively should be considered. This may increase the chances of overall success in controlling lantana, especially in the subtropical areas of South Africa where lantana retains its leaves all year long, eliminating the lag period.

To meet this end, the sap-sucking mirid *Falconia intermedia* (Distant) (Hemiptera: Miridae) was released into South Africa from Jamaica in 1999. In chapter 2 results showed that there was some varietal impact under laboratory conditions and therefore this chapter investigates whether this varietal performance will be shown under different climatic conditions in the field. This chapter describes a post-release evaluation of this agent at five sites in the Eastern Cape Province following releases made in December 2001.

3.2 Materials and Methods

3.2.1 Study sites

Five experimental sites, each with a nearby control site, were selected to represent a climatic range of the province and to include different lantana varieties (Table 3.1). Even though the control sites were nearby, it is however possible that the conditions were not identical or similar compared to the test sites. The varieties were differentiated using morphological features (leaf characteristics, shoot and main stem characteristics, and mature flower colour). Three of the sites were close to the coast: (1) Whitney Farm, on the R72, towards Alexandria; (2) Port Alfred site on the R72, west of Port Alfred; and (3) on the Blind River, East London. The two inland sites were (4) Lyndhurst Farm, on the road towards the Coombs Valley and (5) Heather Glen Farm, towards Martindale (Fig. 2.1).

Six plants (plant 1-6) were marked as test and control plants at both the test and control treatments of each site. A further six plants, adjacent to the test plants, were marked and destructively sampled monthly at the test treatments of each site to allow samples from the sites to be further evaluated at the laboratory. In December 2001 approximately 2400 nymphs and 2100 adults were released at the test treatment of each site; 200 nymphs and 175 adults on each of the six marked *L. camara* plants, and the same number on six other adjacent plants. The control sites were kept free of *F. intermedia* with sufficient distances between them and the test sites.

Three branches at low, middle and high levels were tagged on each of the six plants at both the test and control treatments. Monthly evaluations were conducted on each site with the same measurements made on both test and control sites. The data from the destructive sample was recorded from the sites' test treatments.

Two sampling techniques were used, sampling technique one and sampling technique two.

3.2.2 Sampling technique 1

During each sampling event, several plant growth and insect population parameters were measured. Plant growth measurements included plant height, branch and internode lengths for the different levels of the marked branches on each plant. The number of shoots, fruits and flowers on the marked branches were also recorded for both treatments as a measure of the plant's reproductive activity. Damage was rated on the remaining leaves of the destructive sample (where total damage = area damaged x intensity of damage) (Table 2.2).

Insect population measurements included counts of hatched and viable eggs on destructive samples taken from the plants adjacent to the test treatments. Adult and nymphal survival was also recorded, to monitor population numbers and give and indication of establishment. Three branches at three different heights, low middle and high, were randomly removed from these trees and the first five leaf pairs of each used as the destructive sample. From the first five leaf pairs, one leaf per pair was removed randomly. The remaining leaves on the branch were returned to the laboratory, placed under a light microscope, and the viable and hatched eggs counted to estimate the insects' reproductive activity. The leaf was then given a rating for the intensity (0-3) and the area (0-4) of any insect damage (Table 2.2).

Table 3.1 A list of the Eastern Cape locations and varieties of *Lantana camara* used in the post-release evaluation of *Falconia intermedia*.

Lantana camara variety	Distinguishing morphological features	Flower colour	Site location	Grid reference Test	Grid reference Control
WP EC1	Leaves large, broad, dark, hairy; shoots hairy and spiny; main stem spiny	White Pink	East London	33°00'23"S 27°54'47"E	33°00'13"S 27°55'28"E
WP EC2	Leaves large, broad, dark, hairy; shoots spiny, main stem spiny	White Pink	Whitney Farm	33°40'43"S 26°35'49"E	33°39'54"S 26°34'06"E
WP EC3	Leaves large, broad, dark, hairy; shoots hairy and spiny, main stem spiny	White Pink	Heather Glen Farm	33°19'28"S 26°47'31"E	33°19'32"S 26°47'20"E
DP EC1	Leaves small, tough, hairy; shoots hairy and spiny; main stem with few spines	Dark Pink	Lyndhurst Farm	33°27'11"S 26°53'10"E	33°27'10"S 26°53'19"E
DP EC2	Leaves small, hairy, tough; shoots shoots spiny; main stem with few spines	Dark Pink	Port Alfred	33°36'16"S 26°52'16"E	33°36'10"S 26°52'12"E

At four of the sites (Heather Glen Farm, East London, Port Alfred and Lyndhurst Farm) certain climatic parameters were also measured. The relative humidity and temperature were recorded using a Hobo PRO8® series data logger. This device takes hourly temperature and %RH. Due to a malfunction in the data loggers at different sites at different times, the climatic data was recorded at all four sites simultaneously only for April 2002, and from September 2002 to December 2003.

Light intensity measurements above and below the canopy were also made using a TopTronic® T630 light meter. Three measurements at the same position above the *L. camara* marked trees, and three below the tree were made monthly from marked points. These measurements indicated the amount of light filtering through the lantana canopy to plants growing underneath a lantana shrub.

The abundance of other plant groups underneath the canopy was also recorded to indicate the efficacy of the insect and its added stress in increasing the growth of the other plant groups through interspecific competition.

3.2.3 Sampling technique 2

The vertical growth of the marked plants over time resulted in the low, middle and high tagged branches no longer being a true reflection of plant performance at the different height levels where measurements were made. For the most part, the low level branches moved even lower into the shade, resulting in inadequate sunlight reception and premature abscission of the leaves. The shrubby and thicket-forming nature of lantana also made it increasingly difficult to locate the tagged branches. To avoid such problems, modifications to the sampling technique were made and used from October 2002 onwards.

In this sampling regime, the six marked plants were retained, but instead of using permanent, tagged branches, the low, middle and high levels were chosen relative to one another on a month-to-month basis. Three square quadrates (0.6m x 0.6m) were placed on the marked plants at the low, middle and high levels relatively. The number of shoots equal to or longer than 15cm, number of flowers and number of seeds within these quadrates were counted and recorded. Samples for both the test treatments (destructive sample) and the insect-free control treatment were taken from the field. Damage measurements, internode length, leaf drop and egg counts were taken from the destructive sample. Leaf drop and internode length was recorded from the control samples. Plant height, light intensity measurement and flora cover beneath the canopy were recorded in the field as before.

Due to the unequal number of data recorded for some variables, the nonparametric Kruskal Wallis ANOVA was used for all variables except average daily temperature and average percentage relative humidity where a one-way ANOVA was used. Endpoint data for both tests and sampling techniques used were analysed at the 5% significance level on the Statistica 6.0® programme. One Kruskal Wallis ANOVA was used for each of the insect population and impact related measurements made, and then means were separated using multiple comparison rank tests. To determine the test and control interaction per site of the other variables, each site was tested separately using a nonparametric Kruskal Wallis ANOVA, and means separated using multiple comparison rank tests.

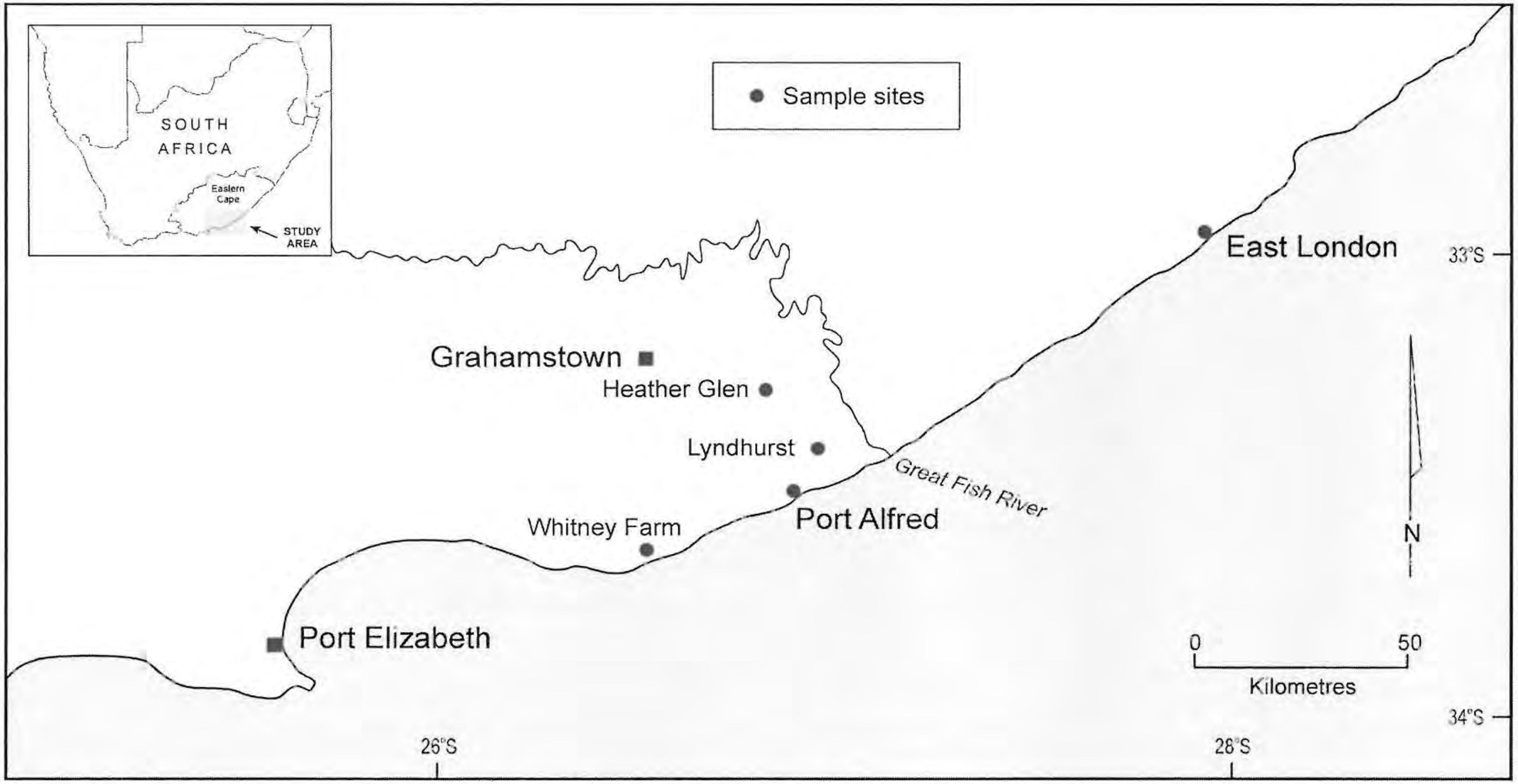

Fig. 3.1 *Lantana camara* sites in the Eastern Cape of *Falconia intermedia* releases.

3.3 Results

3.3.1 Climate

Among the four sites where climatic conditions were observed over the two-year period, Lyndhurst Farm had the highest mean temperature, followed by the East London, Port Alfred and then Heather Glen Farm having the lowest average daily temperature. Lyndhurst Farm recorded significantly higher daily average temperatures than the Heather Glen Farm and Port Alfred sites (Table 3.2). Heather Glen Farm had a significantly lower mean daily temperature of all the sites (Table 3.2). This site experienced the coldest winters of these sites, with temperatures as low as -0.1 °C and -1.9 °C being recorded over the July to September period of 2003. The daily average temperatures over the winter period of 2003 were lower at East London than they were in 2002 over the same period (Fig. 3.2). This may explain the slower increase in mirid individuals over 2003 at this site compared to the Whitney Farm site.

In contrast to the daily average temperatures recorded, Lyndhurst experienced the lowest average percentage relative humidity of all the sites. The highest and second highest daily average relative humidity of the four sites were recorded at the two coastal sites, Port Alfred and East London, respectively. The Port Alfred site had a significantly higher average percentage relative humidity relative to all the other sites.

3.3.2 Establishment

Notwithstanding some insect presence from the time of release until February 2002 at all five sites, *F. intermedia* successfully established at only two of the five release sites, East London and Whitney Farm (Fig. 3.2). No individuals were recorded in the other three sites (Port Alfred, Heather Glen Farm and Lyndhurst Farm) from the post-release field trip undertaken in March 2002. No individuals were recorded for the East London site in April and June 2002, and none at Whitney Farm in February and May 2002. Unlike the other three sites though, this did not signify non-establishment as individuals were recorded in the following months (Figs. 3.2 and 3.3). Despite establishment at the East London site, insect populations persisted in much lower numbers compared to the Whitney Farm site.

Table 3.2 Means (and standard errors) of the average daily temperature and average daily relative humidity at four of the five release sites for the period of 5 April 2002 to 22 April 2002, and 18 September 2002 to 9 December 2003. Means in the same column followed by the same letter are not significantly different ($p > 0.05$, ANOVA, means separated by Newman-Keuls multiple range test).

Site	n	Average Daily Temperature (°C)	Average Daily (% RH)
East London	6	18.97 (0.165) *a*	73.56 (0.428) *a*
Heather Glen Farm	6	17.17 (0.212) *b*	72.94 (0.487) *ab*
Lyndhurst Farm	6	19.18 (0.198) *a*	71.71 (0.515) *b*
Port Alfred	6	18.31 (0.167) *c*	77.86 (0.382) *c*

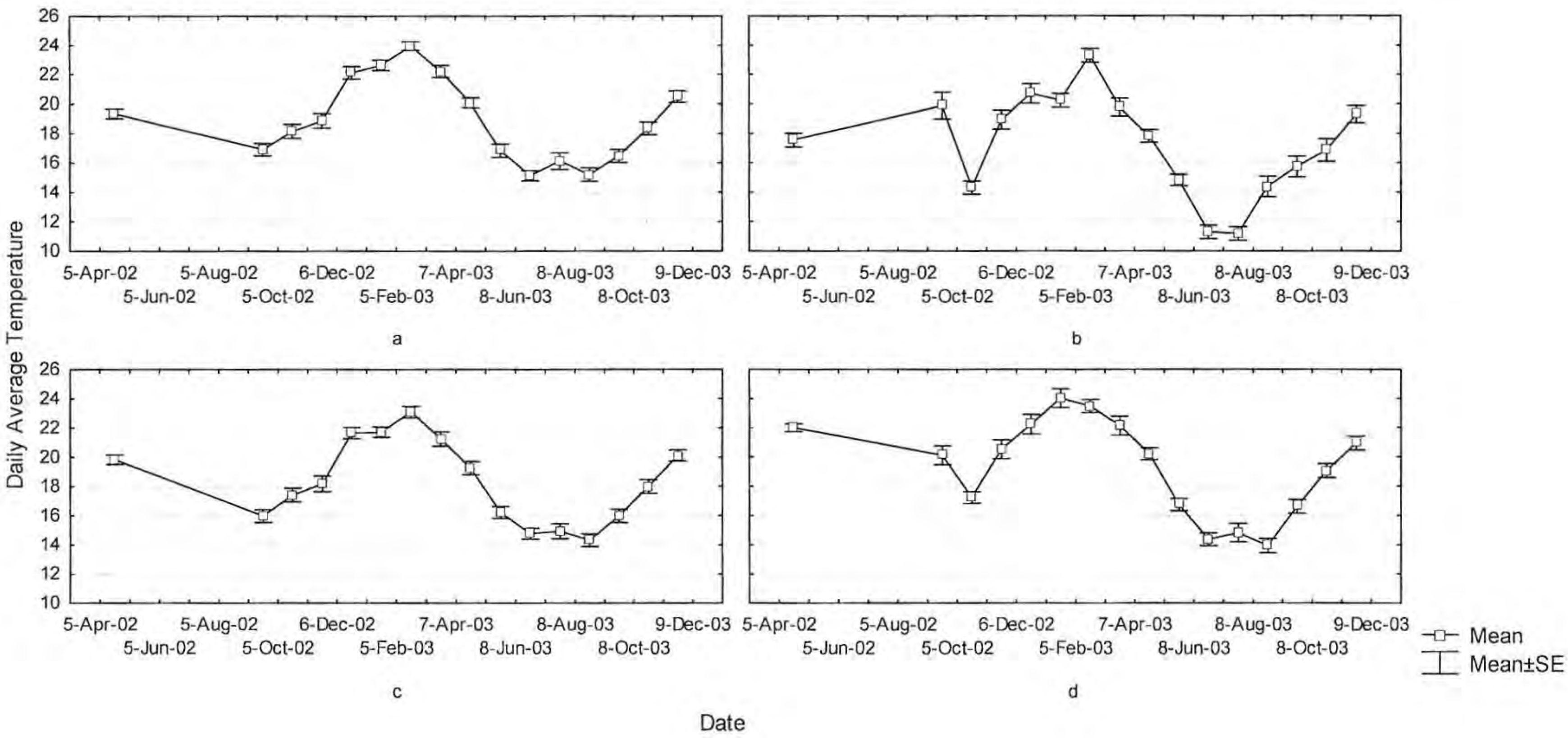

Fig. 3.2 Mean plots of the average daily temperature at four release sites from the 5th April to 22nd April 2002, and 8th September 2002 to 09 December 2003. a = East London, b = Heather Glen Farm, c = Port Alfred, d = Lyndhurst Farm.

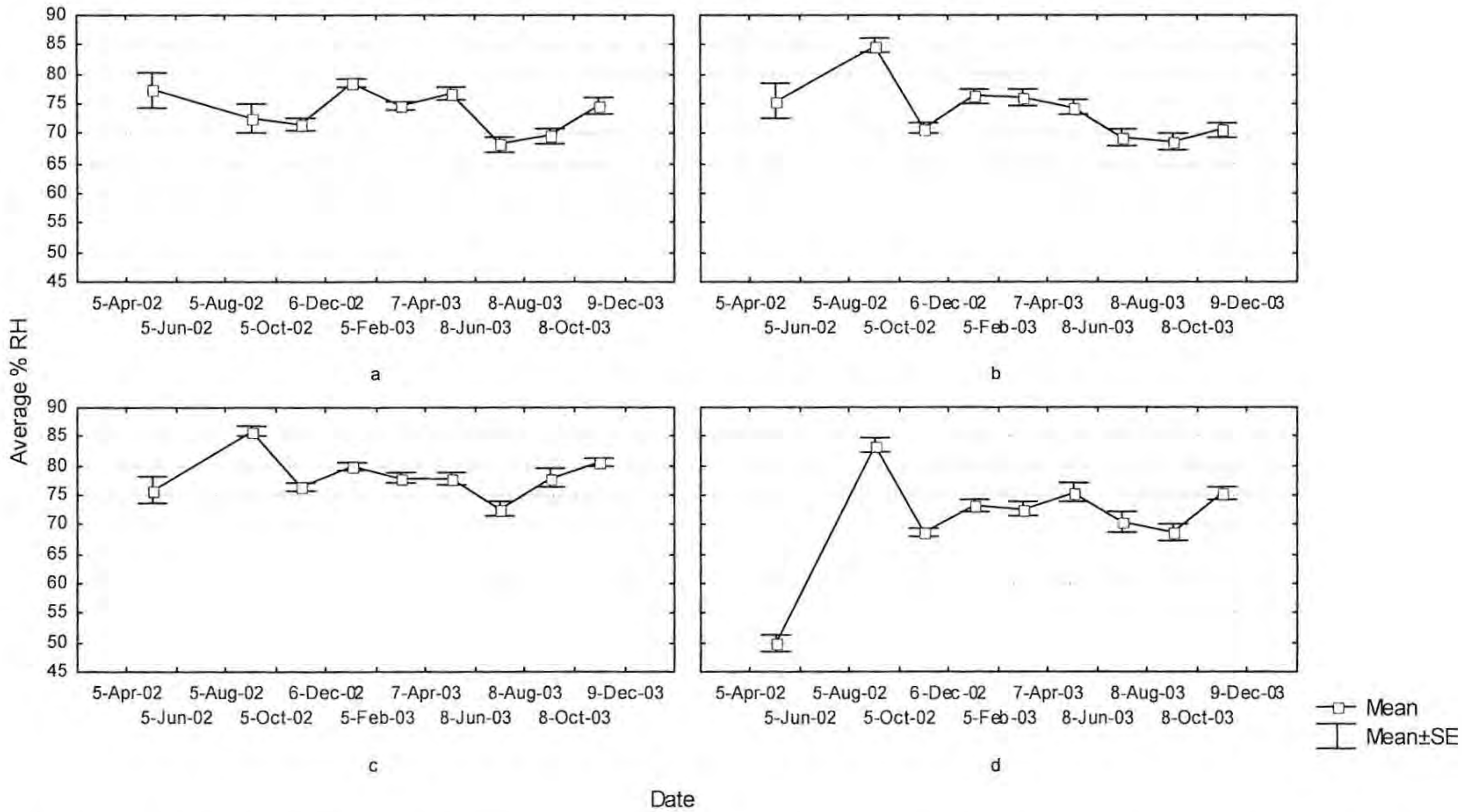

Fig. 3.3 Mean plots of the average daily percentage humidity at four release sites from the 5th April to 22nd April 2002, and 8th September 2002 to 09 December 2003. a = East London, b = Heather Glen Farm, c = Port Alfred, d = Lyndhurst Farm.

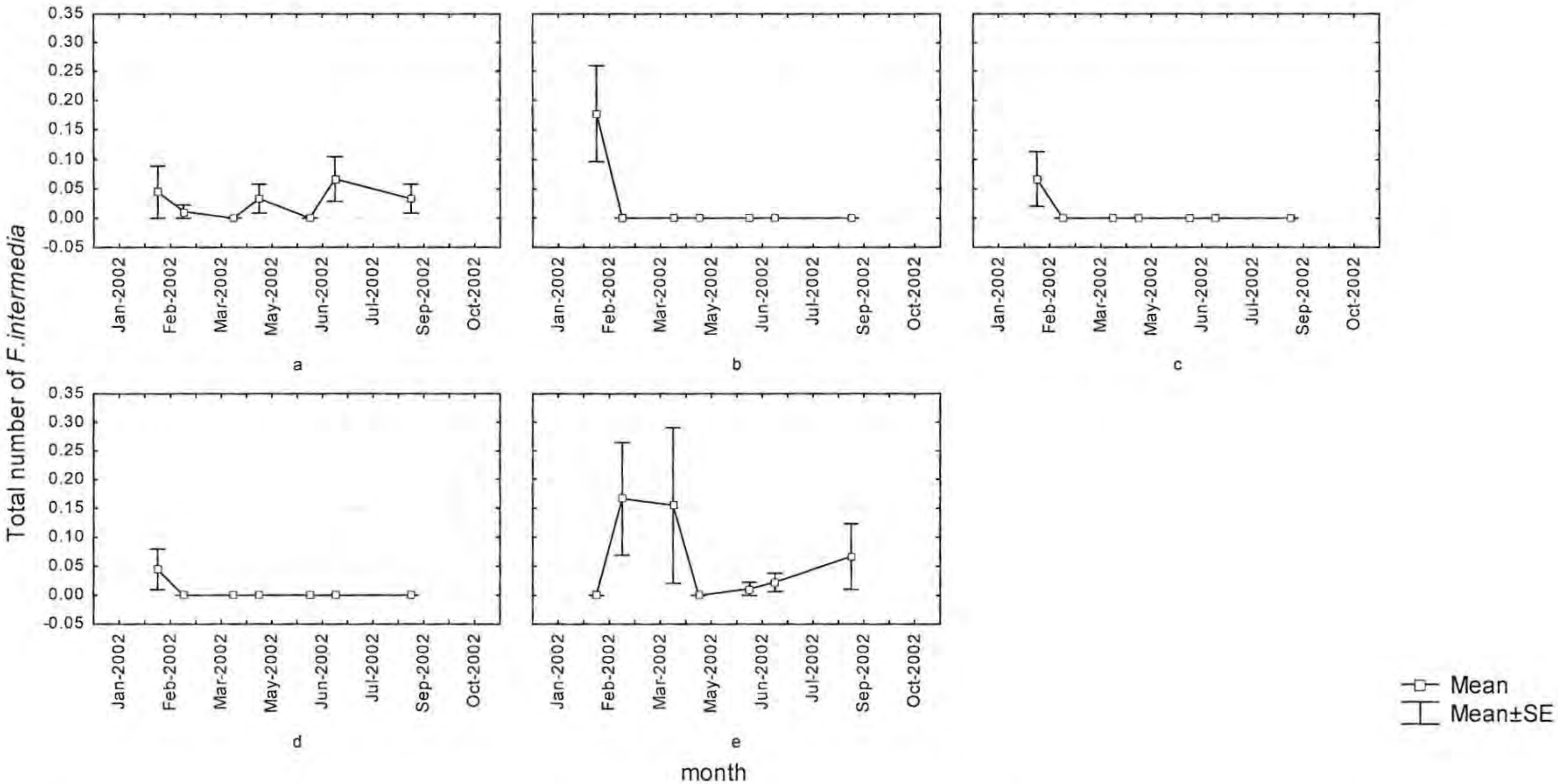

Fig. 3.4 Mean and standard error (denoted by vertical bars) plots of the total number of *Falconia intermedia* individuals on *Lantana camara* trees at test treatments of the five release sites for the period February to September 2002 sampled by technique 1 (a = East London, b = Heather Glen Farm, c = Lyndhurst Farm, d = Port Alfred , e = Whitney Farm).

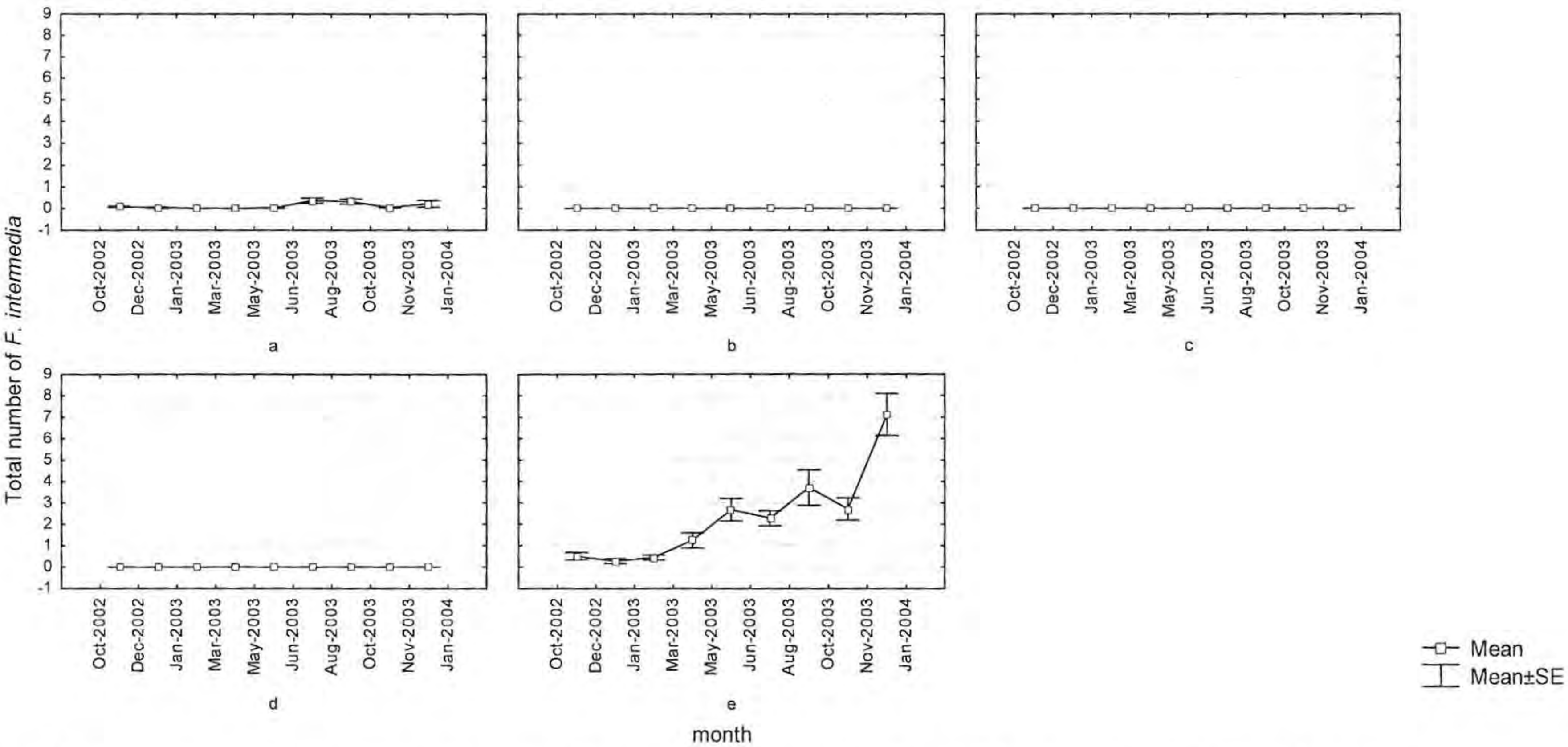

Fig. 3.5 Mean and standard error (denoted by vertical bars) plots of the total number of *Falconia intermedia* individuals on *Lantana camara* trees at the test treatments of the five release sites for the period December 2002 to December 2003 sampled by technique 2(a = East London, b = Heather Glen Farm, c = Lyndhurst Farm, d = Port Alfred , e = Whitney Farm) .

3.3.3 Population Parameters

3.3.3.1 Population numbers (February-September 2002)

The Whitney Farm site had the highest mean population numbers of *F. intermedia* following establishment. It had a mean number of nymphs of 0.04, or 1 nymph in 26 leaf pairs, and a mean number of adults of 0.02, or 1 adult in 45 leaf pairs per plant (Table 3.3). The East London site had a mean number of nymphs of 0.02, or 1 nymph in 57 leaf pairs, and the greatest number of adults with a mean of 0.10, or a single adult in 10.5 leaf pairs. Population numbers were low at Whitney Farm over the cooler winter months of May to August (Fig. 3.4). Prior to the insects disappearing at the other three sites, the population sizes were reasonable. Lyndhurst Farm site had a mean number of nymphs per leaf pair of 0.03, or 1 nymph in 31.5 leaf pairs and a mean number of adults per leaf pair of 0.06, or 1 adult in 16 leaf pairs. Heather Glen Farm had a mean of 0.01 nymphs and adults per leaf pair, or 1 nymph and 1 adult in 79 leaf pairs. Port Alfred had a mean number of nymphs per leaf pair of 0.01, or 1 nymph in 156 leaf pairs but no adults were recorded or detected on the destructive samples. In this period the low population numbers showed no significant differences among the different sites (Table 3.3). The number of hatched and viable eggs recorded at Heather Glen Farm was significantly more than at all the other sites except Whitney Farm (Table 3.3).

3.3.3.2 Population numbers (December 2002-December 2003)

The populations increased in both East London and Whitney Farm sites, where the insect had established. Whitney Farm had significantly more nymphs and adults per leaf pair compared to East London (Table 3.4). At the Whitney Farm site there was a mean number of nymphs of 2.05, or 1 nymph in 1 per leaf pair (2 nymphs per leaf pair) and a mean number of 0.25 adults per leaf pair, or 1 adult in 4 leaf pairs were recorded. The East London site had a mean number of nymphs of 0.12, or 1 nymph in 8 leaf pairs, and a mean number of adults of 0.02, or 1 nymph per 52.5 leaf pairs were recorded. Seasonal conditions once again affected population numbers at Whitney Farm, with population numbers increasing again from September 2003 (Fig. 3.5). The number of hatched and viable eggs recorded at Whitney Farm was significantly more than the number of eggs laid at East London (Table 3.4). This is consistent with the larger population numbers recorded at this site.

Table 3.3 *Falconia intermedia* population parameters in field trials for the test treatments of five Eastern Cape *Lantana camara* varieties for the period of February 2002 to September 2002 using sampling technique 1 (Mean ± S.E.). Means in the same column followed by the same letter are not significantly different ($p > 0.05$, Kruskal-Wallis ANOVA). Means separated using multiple comparison rank tests.

Site	*n*	Nymphs per leaf pair	Adults per leaf pair	No. of viable eggs	No. of emerged eggs
East London	6	0.02 (0.01)*a*	0.10 (0.06)*a*	0.18 (0.03)*ab*	0.74 (0.07)*a*
Heather Glen Farm	6	0.01 (0.01)*a*	0.01 (0.01)*a*	0.05 (0.02)*ab*	1.38 (0.17)*a*
Port Alfred	6	0.01 (0.01)*a*	0*a*	0.07 (0.02)*ab*	0.69 (0.13)*b*
Lyndhurst Farm	6	0.03 (0.00)*a*	0.06 (0.01)*a*	0.10 (0.03)*b*	0.42 (0.07)*c*
Whitney Farm	6	0.04 (0.02)*a*	0.02 (0.01)*a*	0.28 (0.04)*a*	1.10 (0.14)*a*

Table 3.4 Means (and standard errors) of *Falconia intermedia* population parameters in field trials of the test treatments of five Eastern Cape sites *Lantana camara* varieties for the period of December 2002 to December 2003 using sampling technique 2. Means in the same column followed by the same letter are not significantly different ($p > 0.05$, Kruskal-Wallis ANOVA). Means separated using multiple comparison rank tests.

Site	*n*	Nymphs per leaf pair	Adults per leaf pair	No. of viable eggs	No. of emerged eggs
East London	6	0.12 (0.03) *a*	0.02 (0.01) *a*	0.30 (0.05) *a*	0.53 (0.06) *a*
Heather Glen Farm	6	0 *a*	0 *a*	0 *c*	0 *c*
Port Alfred	6	0 *a*	0 *a*	0 *c*	0 *c*
Lyndhurst Farm	6	0 *a*	0 *a*	0 *c*	0 *c*
Whitney Farm	6	2.05 (0.18) *b*	0.25 (0.01) *b*	5.15 (0.40) *b*	4.62 (0.35) *b*

3.3.4 Impact

3.3.4.1 Damage (February-September 2002)

Most of the leaf-feeding damage inflicted by *F. intermedia* was at Heather Glen Farm, East London and Whitney Farm (Table 3.5). There were no significant differences in total damage at these three sites, but the other two sites (Port Alfred and Lyndhurst Farm) had significantly less mirid damage by comparison (Table 3.5). All five sites experienced a seasonal decrease in total damage by the insect from May 2002 until September 2002 (Fig. 3.6).

3.3.4.2 Damage (December 2002-December 2003)

The Whitney Farm trees had more than four times as much damage as East London in this period using technique 2. This site had a damage index of 3.14, significantly higher than East London's damage index of 0.69 (Tables 3.5, Fig. 3.7). This significant difference was expected as the population numbers in Whitney Farm were much higher than at East London. Due to non-establishment at the other three sites, there was no damage recorded at these sites in this period. The gradual increase in total damage by the mirid *F. intermedia* that was observed at Whitney Farm from January to late May 2003 slowed down slightly from the colder June to mid August months but did not decrease. The East London site was affected by the season though, recording very low total damage over the June and July period and an increase in damage from September 2003.

Table 3.5 Means (and standard errors) of the total feeding damage on *Lantana camara* by *Falconia intermedia* for the five Eastern Cape sites for the period February 2002 to September 2002 using sampling technique 1 (ST1), and for the period December 2002 to September 2003 using sampling technique 2 (ST2). Means in the same column followed by the same letter are not significantly different ($p > 0.05$, Kruskal-Wallis ANOVA). Means were separated using multiple comparison rank tests.

Site	n	Feeding damage (ST1)	Feeding damage (ST2)
East London	6	1.77 (0.11) *a*	0.69 (0.05) *a*
Heather Glen Farm	6	1.92 (0.13) *a*	0.0 (0.00) *c*
Lyndhurst Farm	6	0.81 (0.09) *b*	0.0 (0.00) *c*
Port Alfred	6	0.68 (0.08) *b*	0.0 (0.00) *c*
Whitney Farm	6	1.58 (0.11) *a*	3.14 (0.13) *b*

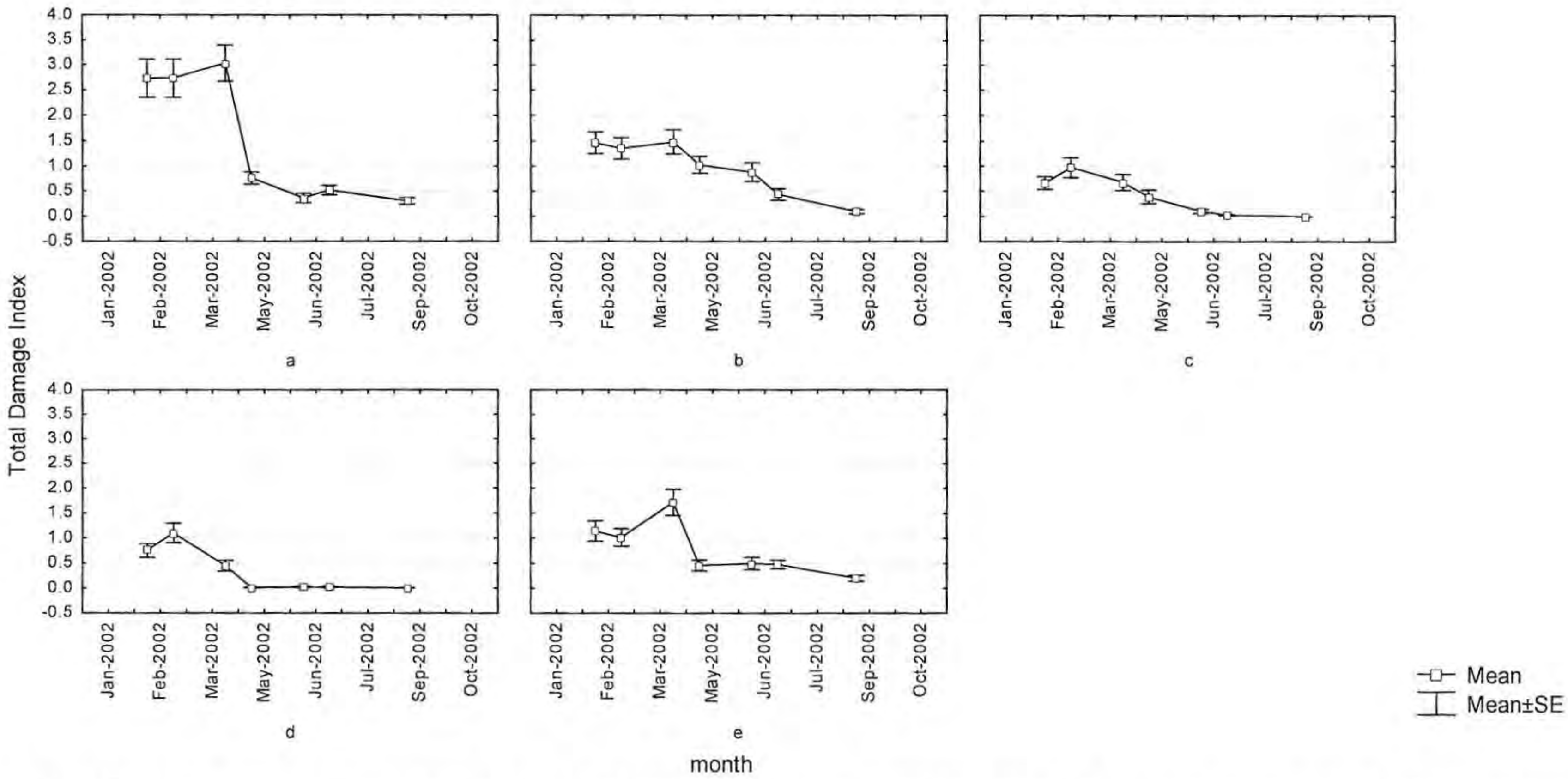

Fig. 3.6 Means and standard error (denoted by vertical bars) plots of the total feeding damage by *Falconia intermedia* individuals on *Lantana camara* trees at the test treatments of the five release sites for the period February to September 2002 sampled by technique 1 (a = East London, b = Heather Glen Farm, c = Lyndhurst Farm, d = Port Alfred, e = Whitney Farm).

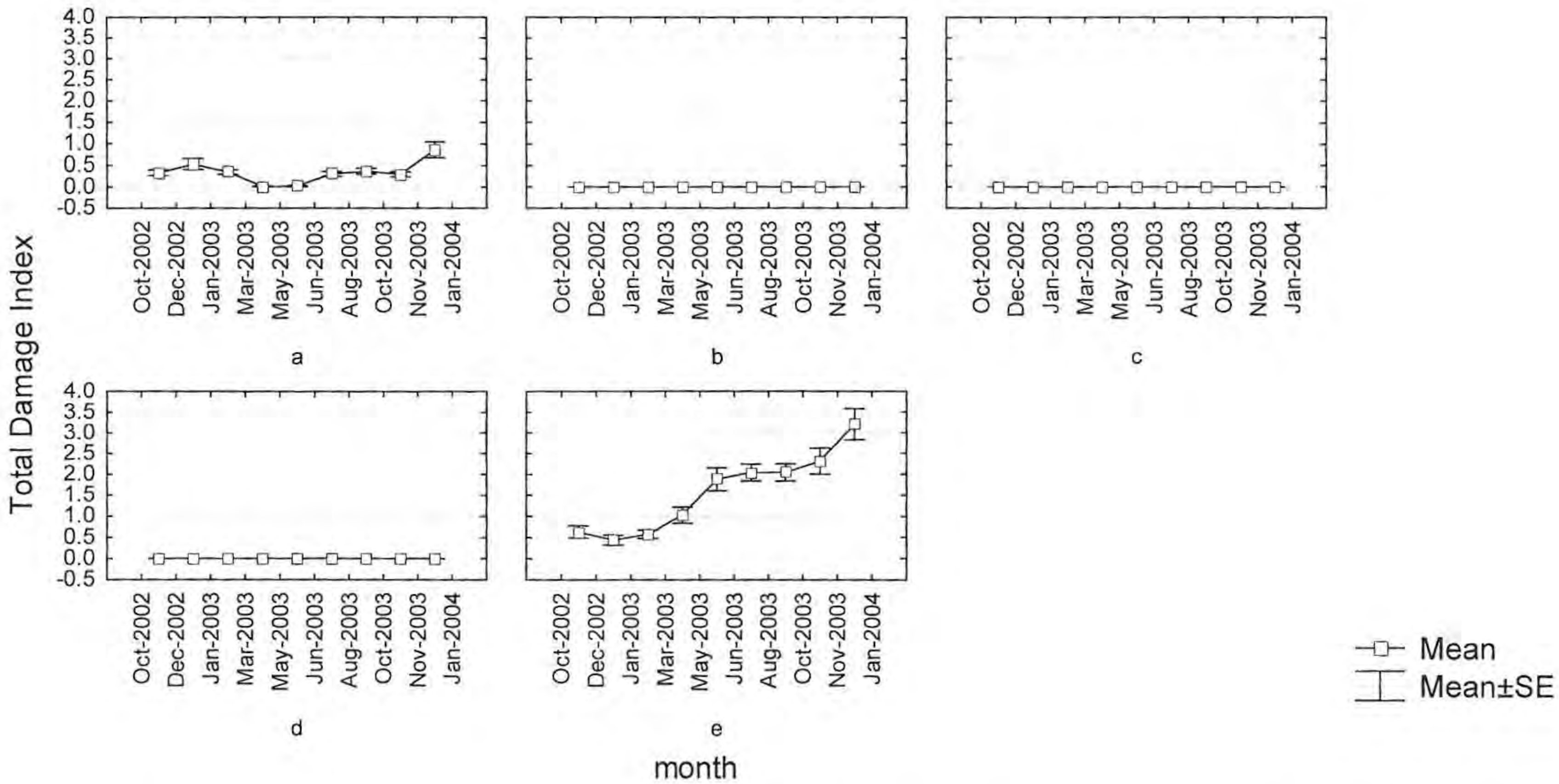

Fig. 3.7 Mean and standard error (denoted by vertical bars) plots of the total feeding damage by *Falconia intermedia* individuals on *Lantana camara* trees at the test treatments of the five release sites for the period December 2002 to December 2003 sampled by technique 2 (a = East London, b = Heather Glen Farm, c = Lyndhurst Farm, d = Port Alfred, e = Whitney Farm).

3.3.5 Impact of *Falconia intermedia* on *Lantana camara* growth

3.3.5.1 Percentage *Lantana camara* cover

The cover of *L. camara* at the two sites where there was establishment of *F. intermedia* showed different responses to the feeding activities of these insects. Whitney Farm had the larger insect population of the two sites. Insect feeding resulted in *L. camara* plants at the test treatment having significantly less cover than at the control treatment of this site (Table 3.6). This is even more impressive considering that the test treatment is located along an irrigation waterway, giving it access to water more readily than the control treatment plants, which were more dependent on rain for moisture.

The East London test site, with insect populations persisting in small numbers throughout the time of the experiment, had a significantly greater cover of lantana at the test treatment. It is unclear whether compensatory growth due to mirid feeding damage was to some degree the cause of this. The different growth rates of *L. camara* at the two treatments, and the influence of the significantly greater cover of herbaceous and creeper plants over lantana bushes at the control treatment (Table 3.11) may have been responsible.

The *L. camara* cover at two of the three remaining sites, Heather Glen Farm and Lyndhurst Farm, was not significantly different. Even though the test treatment at the Port Alfred site had significantly lower *L. camara* cover than the control treatment, it was clearly not due to the feeding damage of *F. intermedia*. The severity of the cooler months, along with increased *T. scrupulosa* damage in February and March 2003, were both factors contributing to the reduced lantana cover at this site.

Table 3.6 Means (and standard errors) of the *Lantana camara* growth parameters between test and control treatment plants of the five Eastern Cape sites for the period November 2001 to December 2003 (Mean ± SE). Means followed by NS = no significant difference ($p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, between a variety's treatments (Kruskal-Wallis ANOVA). Means separated by multiple comparison rank tests.

Site	Treatment	n	% *L. camara* cover	Plant Height (m)	Light intensity under (x100 Lux)
East London	Test	6	74.64 (1.72)	2.99 (0.07)	46.92 (4.18)
	Control	6	66.68 (19.95) **	2.71 (0.08) **	31.09 (3.39) ***
Heather Glen Farm	Test	6	64.22 (1.72)	3.26 (0.08)	22.22 (1.55)
	Control	6	65.32 (1.92) NS	3.13 (0.04) NS	110.95 (8.98) ***
Lyndhurst Farm	Test	6	64.48 (1.94)	1.47 (0.02)	204.63 (14.27)
	Control	6	67.06 (1.09) NS	1.65 (0.03) ***	198.97 (13.98) NS
Port Alfred	Test	6	67.70 (1.77)	2.43 (0.03)	152.48 (11.78)
	Control	6	80.55 (1.71) ***	2.47 (0.04) NS	41.85 (3.59) ***
Whitney Farm	Test	6	64.52 (2.15)	2.52 (0.06)	82.96 (9.24)
	Control	6	71.82 (1.43) *	2.79 (0.06) *	105.86 (8.01) ***

3.3.5.2 Numbers of leaves dropped (February 2002- September 2002)

The test treatments at East London, Lyndhurst Farm and Whitney Farm had significantly higher numbers of leaves dropped in comparison to their control treatments (Table 3.7). The result at Lyndhurst Farm must be interpreted with caution though, as the leaves dropped were not due to *F. intermedia* feeding activity. The high infestations of the lace bug *T. scrupulosa* observed during this insect's population peaks over February to April at this site could be credited with this result. The distribution of the tingid bug was coincidentally more at the test treatment, resulting in the possibly misleading interpretation that the leaves dropped here were linked to *F. intermedia* feeding damage. There was no significant difference in the numbers of leaves dropped at the treatments at Port Alfred and Heather Glen Farm. Sites generally experienced an increase in the number of dropped leaves from April to about August 2002 (Fig. 3.8). It is interesting to note that plants at the Heather Glen site dropped more leaves than at all other sites. The severity of the colder season on *L. camara* and subsequently on any biological control agent that lack of over-wintering mechanisms is once again highlighted at this site.

3.3.5.3 Numbers of leaves dropped (December 2002- December 2003)

There were no significant differences in the treatments at the two sites where the insects established (Table 3.8). Plants at Heather Glen Farm dropped significantly more leaves at its control treatment than at its test treatment. The Lyndhurst Farm test treatment dropped significantly more leaves than its control treatment. The feeding damage of *T. scrupulosa* at Lyndhurst resulted in the test treatment dropping significantly more leaves than the control treatment, as *F. intermedia* failed to establish at this site. *Teleonemia scrupulosa* is widely established in the Eastern Cape, however its feeding damage is easily distinguishable from that of the mirid.

3.3.5.4 Plant height

The plants at Whitney Farm were significantly shorter at the test treatment than at the control treatment (Table 3.6). The East London site had significantly taller *L. camara* bushes at the test treatment than at the control treatment ($H(1, N = 251) = 7.7657$, $p = 0.005$). It is unlikely that this is due to insect feeding damage triggering compensatory growth in the *L. camara* test treatment bushes because insect numbers and feeding damage were both minimal.

Table 3.7 Means (and standard errors) of the *Lantana camara* growth parameters between the test and control treatment plants of the five Eastern Cape sites for the period February 2002 to September 2002 using sampling technique 1. Means followed by NS = no significant difference ($p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, between a variety's treatments (Kruskal-Wallis ANOVA). Means separated by multiple comparison rank test.

Site	Treatment	n	Leaf drop index	Internode Length (cm)	Branch Length (cm)
East London	Test	6	0.82 (0.04)	33.03 (0.72)	68.188 (2.54)
	Control	6	0.67 (0.03) *	30.44 (0.69) *	68.279 (2.32) NS
Whitney Farm	Test	6	0.64 (0.03)	30.873 (0.697)	75.69 (1.78)
	Control	6	0.53 (0.03) *	38.021 (1.156) *	60.99 (1.38) ***
Heather Glen Farm	Test	6	1.15 (0.04)	27.583 (0.73)	53.66 (1.28)
	Control	6	1.06 (0.04) NS	32.515 (0.81) ***	48.08 (0.97) **
Lyndhurst Farm	Test	6	0.83 (0.04)	20.54 (0.681)	55.12 (1.456)
	Control	6	0.55 (0.03) ***	19.44 (0.494) *	48.08 (1.024) **
Port Alfred	Test	6	1.01 (0.04)	23.08 (0.53)	53.88 (1.05)
	Control	6	0.95 (0.04) NS	31.86 (0.74) ***	64.87 (1.22) ***

3.3.5.5 Branch length (February 2002- September 2002)

Even though damage by leaf-feeding biological control agents, such as *T. scrupulosa*, may result in the dieback of nodes and even whole branches (Cilliers and Neser 1991), the results obtained at these sites were the opposite. The mean lengths of the marked *L. camara* branches were significantly longer at the test than at the control treatments at all sites except East London (Table 3.6). Whether the plants at test treatment were growing faster due to the plant compensating is unlikely, as the period of attack and the magnitude of feeding damage were both moderate.

Table 3.8 Means (and standard errors) of *L. camara* leaf drop and internode length between test and control treatment plants for the period December 2002 to December 2003 using sampling technique 2. Means followed by NS = no significant difference ($p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, between a variety's treatments (Kruskal-Wallis ANOVA). Means separated by multiple comparison rank tests.

Site	Treatment	n	Leaf drop Index (cm)	Internode Length (cm)
East London	Test	6	0.19 (0.02)	36.97 (0.74)
	Control	6	0.17 (0.01) NS	39.11 (0.75) *
Heather Glen Farm	Test	6	0.40 (0.02)	38.46 (0.79)
	Control	6	0.59 (0.03) **	37.73 (0.74) NS
Lyndhurst Farm	Test	6	0.36 (0.02)	29.03 (0.52)
	Control	6	0.15(0.02) ***	27.36 (0.46) NS
Port Alfred	Test	6	0.16 (0.01)	26.60 (0.44)
	Control	6	0.17 (0.01) NS	33.381(0.51) ***
Whitney Farm	Test	6	0.15 (0.01)	39.05 (0.66)
	Control	6	0.15 (0.01) NS	40.67 (0.71) NS

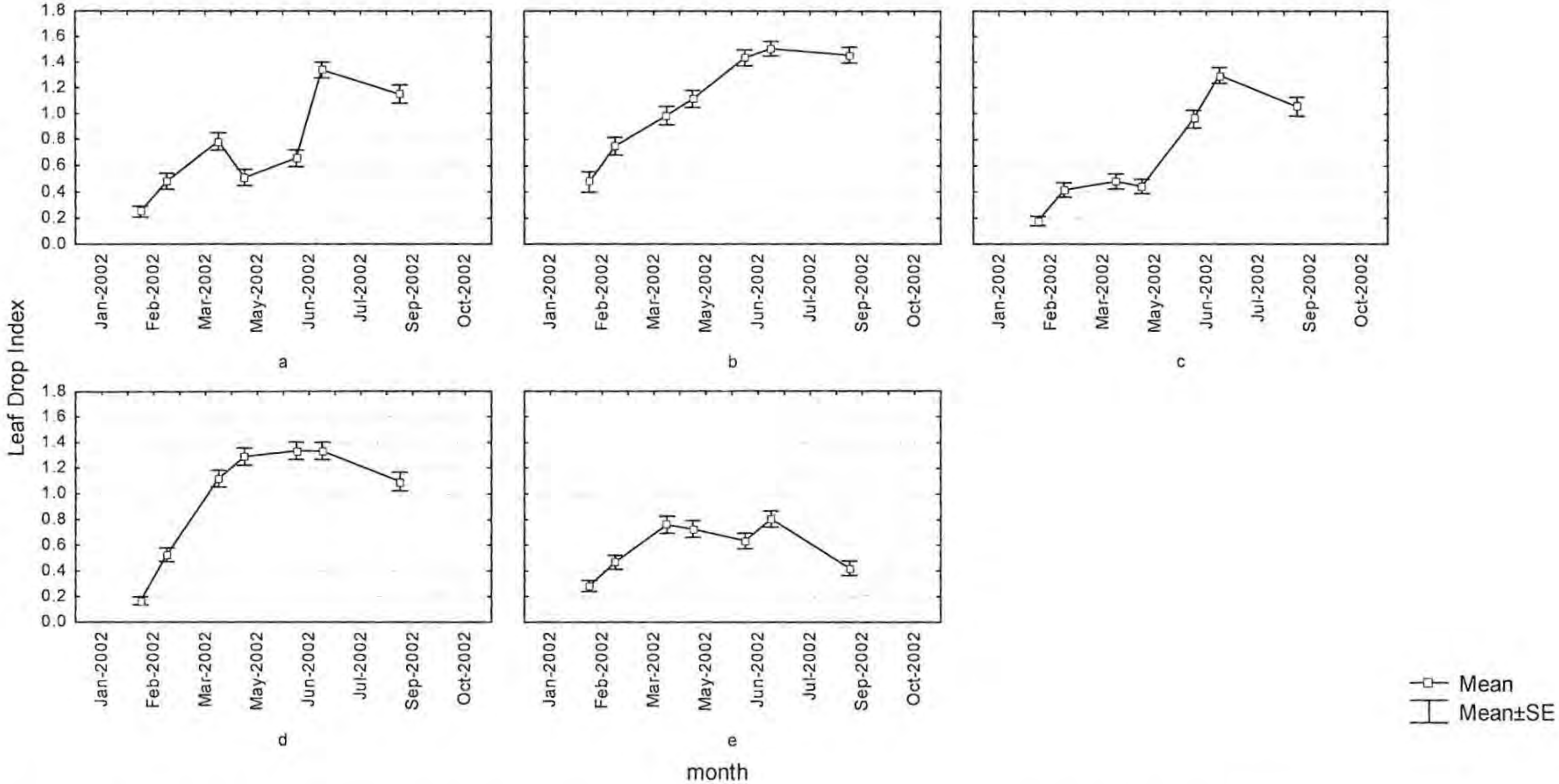

Fig. 3.8 Means and standard error (denoted by vertical bars) plots of the number of leaves dropped per leaf pair by *Lantana camara* trees in the five Eastern Cape sites test and control treatments for the period February to September 2002, data collected using sampling technique 1 (a = East London, b = Heather Glen Farm, c = Lyndhurst Farm, d = Port Alfred, e = Whitney Farm).

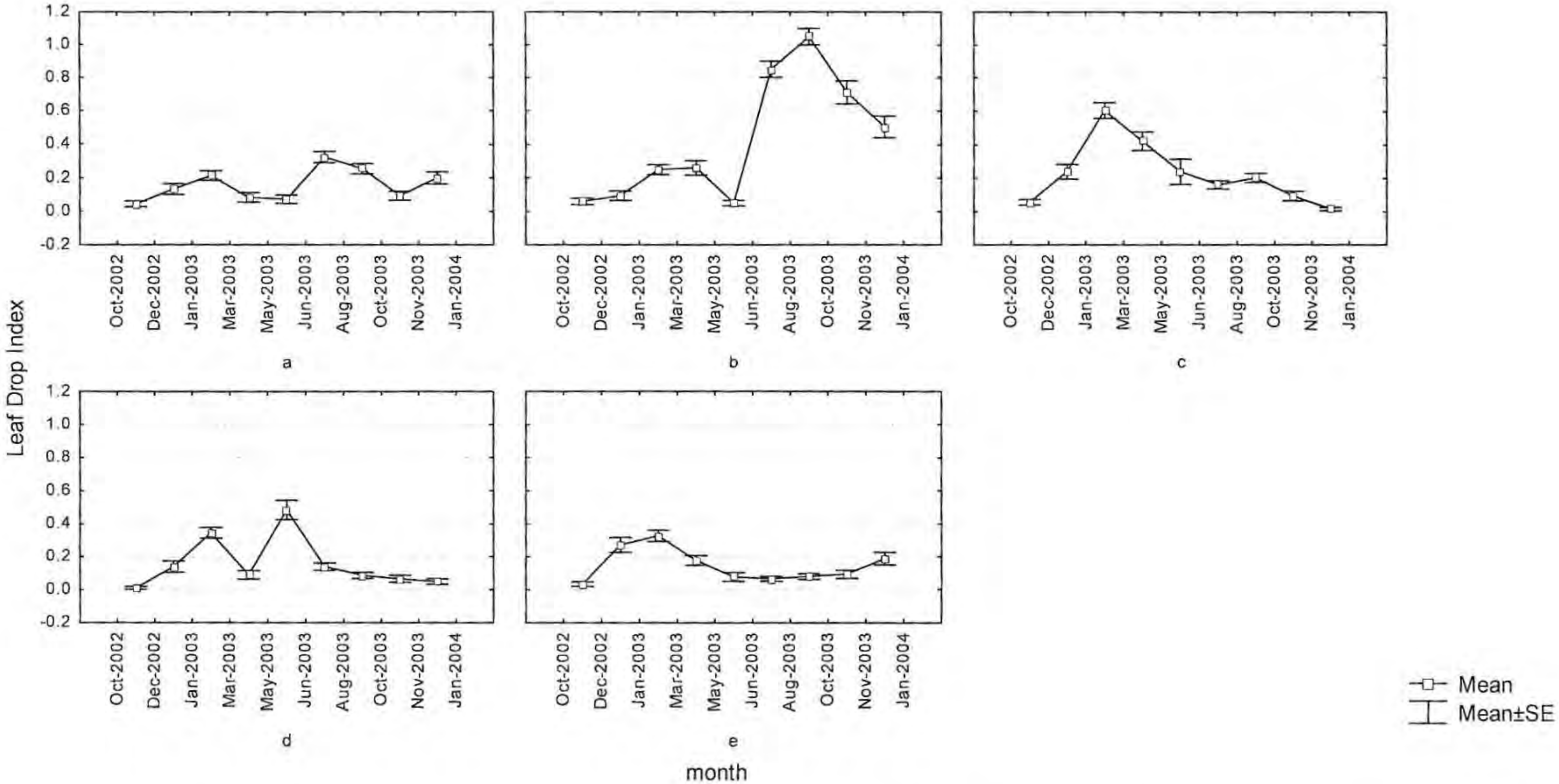

Fig. 3.9 Means and standard error (denoted by vertical bars) plots of the number of leaves dropped per leaf pair by *Lantana camara* trees in the five Eastern Cape sites test and control treatments for the period November 2002 to December 2003, data collected using sampling technique 2 (a = East London, b = Heather Glen Farm, c = Lyndhurst Farm, d = Port Alfred , e = Whitney Farm).

3.3.5.6 Internode length (February 2002- September 2002)

Whitney Farm, the site that had the most number of individuals, produced the most encouraging results. The mean internode lengths measured at the test treatments of Whitney Farm, Heather Glen Farm and Port Alfred, had significantly shorter internodes than those measured at their control treatments (Table 3.7). The East London site had significantly shorter internode lengths on the control treatments than at the test treatment. Lyndhurst Farm showed no significant differences in their treatments over the above period.

3.3.5.7 Internode length (December 2002-December 2003)

Internode lengths at three of the five sites showed no significant difference between the treatments (Table 3.8). Only the Port Alfred and East London sites showed some significant differences in their treatments, with test treatments having significantly shorter internodes than control treatments. Despite non-significance at East London and Whitney Farm, the test treatments at both sites had shorter internodes.

3.3.6 Impact of *Falconia intermedia* on reproductive ability of *Lantana camara*

3.3.6.1 Number of flowers (November 2001 – September 2002)

The three coastal sites (East London, Whitney Farm, and Port Alfred) recorded the highest numbers of flowers (Table 3.9). The test treatments at Whitney Farm and East London particularly produced a greater amount of flowers than control treatments, but only at Whitney Farm were the flowers significantly more abundant. Favourable climatic conditions at these coastal sites allow for continuous production of flowers throughout the year, allowing for these to have cumulatively more flowers and seeds. The other three sites yielded flowers that had no significant differences between their test and control treatments (Table 3.9).

Table 3.9 Means (and standard errors) of the reproductive growth of *Lantana camara* between test and control treatment plants for the period November 2001 to September 2002 using sampling technique 1. Means followed by NS = no significant difference ($p > 0.05$), *** = $p < 0.001$, between a variety's treatments (Kruskal-Wallis ANOVA). Means separated by multiple comparison rank tests.

Site	Treatment	n	Number of flowers	Number of seeds
East London	Test	6	4.12 (0.86)	6.45 (0.97)
	Control	6	3.19 (0.69) NS	5.96 (1.04) NS
Heather Glen Farm	Test	6	0.51 (0.13)	0.79 (0.18)
	Control	6	0.38 (0.09) NS	1.13 (0.24) NS
Lyndhurst Farm	Test	6	0.56 (0.13)	1.15 (0.26)
	Control	6	0.75 (0.15) NS	1.31 (0.26) NS
Port Alfred	Test	6	1.34 (0.31)	2.14 (0.59)
	Control	6	1.64 (0.42) NS	2.73 (0.63) NS
Whitney Farm	Test	6	5.87 (0.88)	13.82 (1.76)
	Control	6	1.58 (0.34) ***	2.391 (0.60) ***

3.3.6.2 Number of flowers (November 2002 – December 2003)

A similar trend to the one observed using technique 1 was again observed in the number of flowers. The coastal sites produced more flowers than the two inland sites (Table 3.10). The Whitney Farm test treatment had significantly greater number of flowers than its control treatment. There were no significant differences in the test and control treatments at all of the other sites. It seems that the added variable of feeding damage has resulted in the increased production of flowers at Whitney Farm.

Table 3.10 Means (and standard errors) of the reproductive growth of *Lantana camara* between test and control treatment plants for the period December 2002 to December 2003 using sampling technique 2. Means followed by NS = no significant difference ($p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, between a variety's treatments (Kruskal-Wallis ANOVA). Means separated by multiple comparison rank tests.

Site	Treatment	n	Number of flowers	Number of seeds
East London	Test	6	10.15 (0.99)	19.27(1.81)
	Control	6	8.03 (0.70) NS	11.05 (1.16) *
Heather Glen Farm	Test	6	5.24 (0.65)	6.83 (0.85)
	Control	6	5.42 (0.68) NS	9.46 (1.08) NS
Lyndhurst Farm	Test	6	5.21 (0.56)	8.68 (0.78)
	Control	6	5.29 (0.49) NS	9.00 (0.88) NS
Port Alfred	Test	6	11.41 (0.95)	12.24 (1.24)
	Control	6	14.68 (1.37) NS	14.18 (1.33) NS
Whitney Farm	Test	6	12.25 (1.17)	17.265 (1.68)
	Control	6	4.11 (0.48) ***	7.662 (0.84) ***

3.3.6.3 Number of seeds (November 2001- September 2002)

The coastal sites produced more seeds than the inland sites, with Whitney Farm plants producing significantly greater number of seeds at the test treatment than the control (Table 3.9) (H (1, N = 279) = 58.2298, p = 0.000). The other sites all had no significant differences in the number of seeds produced between their treatments.

3.3.6.4 Number of seeds (November 2002 – December 2003)

The two sites where there was establishment of *F. intermedia*, Whitney Farm (H (1, N = 468) = 8.2796, p = 0.000) and East London (H (1, N = 468) = 6.6467, p = 0.009) produced significantly greater numbers of seeds at their test treatments than on their control treatments (Table 3.10). The other three sites showed no significant differences in the number of seeds produced between the different treatments. It is possible that the insect feeding triggered compensatory growth and/or reproductive output in these two sites, leading to greater numbers of seeds in these two treatments.

3.3.7 Impact of *Falconia intermedia* on floral growth beneath *Lantana camara*

3.3.7.1 Light intensity under *Lantana camara*

Continuous and severe damage by an insect agent is expected to increase the number of leaves dropped at the test treatment of the sites. This in turn results in a decrease in *L. camara* cover of affected trees and an increase in the amount of light filtering through to the floral layer underneath lantana. Consequently an increase in growth at the ground level occurs, as well as an increase in the photosynthetic and competitive ability of these plants relative to lantana. Plants underneath the lantana bushes at Whitney Farm (H (1, N = 732) = 94.8431, p = 0.000) and Heather Glen Farm (H (1, N = 684) = 139.6233, p = 0.000) received a significantly greater amount of light at their control than their test treatments, but East London (H (1, N = 681) = 38.0290, p = 0.000) and Port Alfred (H (1, N = 702) = 130.8394, p = 0.000) both had significantly greater light intensities at their test treatment. There was no significant difference in light intensity at the test and control treatment at Lyndhurst Farm (Table 3.6). A significantly greater cover of trees, herbaceous plants and creeper (Table 3.11) at the test treatment of Heather Glen Farm affected not only the lantana itself, but was responsible for the significantly lower light readings in this treatment.

3.3.7.2 Number of *L. camara* seedlings

Considerably more *L. camara* seedlings were produced at the control treatment of the Whitney Farm site than at the test treatment (H (1, N = 252) = 57.7124, p = 0.000) (Table 3.11). The other four sites had similar numbers of seedlings at their test and control treatments.

3.3.7.3 Percentage grass cover

A significant greater percentage cover of grasses was recorded at the Whitney Farm test treatment than at its control treatment, notwithstanding the greater amount of light filtering through to the grasses beneath the controls (Table 3.11). Even though this result is largely due to the feeding damage and increased leaf drop at the test treatment, the slightly better moisture conditions levels at the test treatments may also have played a role. The Port Alfred and East London test treatments also hosted a significantly greater percentage of grass cover. The other two sites (Lyndhurst Farm and Heather Glen Farm) showed no significant differences.

3.3.7.4 Percentage herbaceous plant cover

All sites had significant differences of herbaceous plants in their treatments. Test treatments at Whitney Farm, Heather Glen Farm and Port Alfred had significantly higher percentages of herbaceous plant cover than their control treatments (Table 3.11). The East London and Lyndhurst Farm sites however, had significantly lower percentage cover of herbaceous plants at their test treatments compared to their controls. A significantly less abundant cover of *L. camara*, trees and the significantly greater cover of creeper at the East London control treatment influenced this result (Table 3.11). The herb cover at the Lyndhurst Farm was not significantly different between the two treatments.

3.3.7.5 Percentage creeper cover

A combination of insect feeding damage and moist conditions at the test treatment of Whitney Farm resulted in this treatment having highly significant creeper cover than its control (H (1, N = 249) = 49.3509, p = 0.000) (Table 3.11). The East London site experienced the opposite result, with the test treatment being covered by significantly less creeper than the associated control (H (1, N = 251) = 49.5819, p = 0.000). As with the percentage herbaceous plant cover, the Heather Glen Farm site recorded significantly higher percentage of creepers at its test than its control treatment (H (1, N = 251) = 17.4152, p = 0.000). The other two sites, Lyndhurst Farm and Port Alfred, had similar creeper cover at their treatments.

3.3.7.6 Percentage tree cover

East London's control treatment had a significantly greater percentage tree cover than the test (H (1, N = 251) = 24.0474, p = 0.000) (Table 3.11). A significantly greater cover of trees at the test than the associated control treatment roofed the Heather Glen site (H (1, N = 252) = 38.6085, p = 0.000). This is one of the primary factors resulting in the significantly higher mean light intensity at the control treatment (Table 3.6). Tree cover at the test treatment of Port Alfred was also significantly higher than at the control treatment (H (1, N = 252) = 23.2835, p = 0.000). Whitney Farm recorded no significant differences in its treatments over the trial period.

Table 3.11 Means (and standard errors) of the flora growth underneath the *Lantana camara* between test and control treatment plants for the period November 2001 to December 2003. Means followed by NS = no significant difference ($p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, between a variety's treatments (Kruskal-Wallis ANOVA). Means separated by multiple comparison rank tests.

Site	Treatment	n	No. of *L. camara* seedlings	% Grasses	% Herbaceous plants	% Creepers	% Trees
East London	Test	6	0.05 (0.03)	7.35 (1.18)	27.22 (2.21)	24.61 (2.31)	10.41 (2.23)
	Control	6	0.02 (0.02) NS	4.20 (1.02) ***	43.70 (2.82) ***	49.62 (2.65) ***	25 (2.80) ***
Heather Glen Farm	Test	6	0.33 (0.14)	5.89 (0.61)	43.83 (2.25)	9.80 (1.29)	55.02 (3.40)
	Control	6	0.99 (0.27) NS	8.51 (0.91) NS	27.43 (1.50) ***	4.05 (0.88) ***	25.36 (2.78) ***
Lyndhurst Farm	Test	6	0.095 (0.05)	13.460 (1.15)	19.19 (1.38)	2.43 (0.64)	2.10 (0.81)
	Control	6	0.024 (0.02) NS	12.68 (1.42) NS	21.94 (1.15) *	1.61 (0.47) NS	7.26 (1.33) *
Port Alfred	Test	6	0.39 (0.13)	25.47 (1.99)	23.66 (1.44)	1.79 (0.73)	33.15 (2.20)
	Control	6	0.15 (0.09) NS	13.86 (1.72) ***	6.78 (0.86) ***	0.64 (0.27) NS	19.85 (2.24) ***
Whitney Farm	Test	6	0.08(0.05)	27.74 (2.51)	25.09 (2.18)	25.76 (2.91)	6.58 (1.40)
	Control	6	3.84 (0.70) ***	6.35 (0.89) ***	4.41 (0.55) ***	2.78 (0.66) ***	9.80 (1.97) NS

3.4 Discussion

Climate and elevation has been directly and indirectly implicated in non-establishment of agents in 29% of cases analysed by Broughton (2000). Climatic incompatibility was also cited by other researchers to be a limiting factor to the establishment, distribution and effectiveness of biocontrol agents (Cilliers and Neser 1991, Day and Neser 2000, Day *et al.* 2003). The establishment of *F. intermedia* at two of the three coastal sites where releases were made suggest that the different climatic conditions among the sites played a role in establishment. The warmer and humid conditions, the smaller variation in average temperature throughout the year, and the moist conditions at the coastal sites make for more ideal conditions for the survival of the mirid. In such conditions lantana can retain its leaves throughout the year, thereby eliminating the lag period when populations of biological control agents must recover. The conditions also allow the leaf-feeding *F. intermedia* to increasingly damage lantana throughout the year, as was the case at Whitney Farm (Fig. 3.7). Despite conditions being slightly more ideal at coastal than inland sites for lantana growth and *F. intermedia* survival, seasonal conditions still affected population numbers at Whitney Farm, with population numbers decreasing over the July-August 2003 winter (Fig. 3.5).

Adverse climatic conditions appear to have been responsible for non-establishment at the Heather Glen Farm site. Heather Glen Farm lantana was predominantly a white pink variety similar to the one at East London where insects established. The WP EC3 variety from Heather Glen Farm was preferred for oviposition in the laboratory trials conducted in Chapter 2. Indeed, the total number of eggs at Heather Glen Farm in the field trails was higher than at all the other sites, despite populations being wiped out by March 2002, and egg production at Whitney Farm and East London continuing until September 2002, the end of the trial period using sampling technique 1. However, the East London and Heather Glen Farm sites experienced significantly different temperature ranges between the two sites over the year 2002. Temperatures of 5°C and below, such as those experienced by Heather Glen Farm over the autumn and winter seasons, are not adequate for the growth of lantana (Swarbrick *et al.* 1995) and are therefore not suitable temperatures for the survival of *F. intermedia*. Such low temperatures may slow vital physiological processes in insects and reduce the potential rate of population growth. The performance of *F. intermedia* at East London was most likely also affected in this way by lower average temperatures recorded over 2003. Adverse weather conditions added to the lack of over wintering mechanisms by *F. intermedia* insect such as adult or pupal diapause, has most likely led to demise of populations at Heather Glen. Not only do harsh weather conditions have an effect on the agent, but they can also alter the characteristics of a plant host, especially by defoliation, that would otherwise have been a suitable host (Day *et al.* 2003). Insect population numbers are either wiped out completely, or are greatly reduced during the cold winter seasons. Among the five Eastern Cape sites studied, East London and Whitney Farm have proved to be the most adequate release sites for the establishment leaf-feeding insects such as *F. intermedia.* They have appropriate climatic conditions and a white pink lantana variety on which the insect performed best in both the laboratory trials (Chapter 2) and these field trials.

Temperatures observed at Port Alfred and Lyndhurst Farm sites were not as cold as the ones experienced by the Heather Glen Farm and thus did not play as big a role in non-establishment. However Port Alfred had significantly higher percentage relative humidity than all the other sites. It is unlikely that this may have contributed in any way to the mirid not establishing at Port Alfred as such percentage relative humidities would not be foreign to *F. intermedia* at its native ranges. Port Alfred and Lyndhurst Farm lantana varieties recorded the lowest total damage, recorded the lowest number of eggs and had the lowest number of individuals. Unlike other sites, where there was an upward trend through the summer seasons, these two sites already experienced a downward trend in population numbers. Furthermore, there was an absence of adults at Port Alfred and very few recorded at Lyndhurst Farm, indicating that the insects possibly did not finish their life cycle on these varieties and that adult mortalities were high. There was some intermittent damage due to *T. scrupulosa* at these two sites, especially over the February to April period (pers. obs.).

Poor plant quality due to soil conditions at these two varieties may be the reason for non-establishment at the two sites. The laboratory trails conducted in chapter 2 showed that *F. intermedia* displayed no varietal preference for any of the varieties from these five Eastern Cape sites, even though there were differences in performance. However, conditions in the laboratory were kept constant and thus sporadic climatic changes eliminated, unlike in the field trials. Furthermore, the soil used to maintain the plants was constantly watered and fertilised. This would have resulted in good soil quality, which consequently would have lead to better plant and leaf quality in the laboratory trails. Indeed the leaves of the lantana in the laboratory trials in both these sites were lighter in colour and were not as tough as the ones experienced by *F. intermedia* under field conditions. The tougher leaves experienced by mirid individuals under field conditions may have been a deterrent to the feeding activity of the insects. Such morphological differences in lantana varieties have been reported to influence the performance of several insect herbivores, with certain varieties of lantana preferred more by some insect herbivores (e.g. *Teleonemia scrupulosa* and *Calycomyza lantanae*) (Harley and Kassulke 1974; Cilliers 1987; Cilliers and Neser 1991; Radunz 1971).

The feeding damage at the most infested and mirid-populated sites, Whitney Farm, increased from 2002 to 2003. This kind of increase proved *F. intermedia*'s potential as a biocontrol agent and its reproductive ability to rapidly increase population numbers. Insect numbers at this site have not peaked yet, as there was still only one nymph per leaf and one adult in four leaf pairs at the end of the field trial. Barring any major short-term climatic changes, such as cold snaps, the population numbers are expected to increase. Despite the fact that populations were not at their peak, feeding damage of the mirid made some landmark impact on *L. camara*, significantly reducing the cover of lantana at the test treatment. Leaves fed on by the mirid abscised prematurely, sometimes not requiring severe damage for this to happen. A moderate breeze, some rain and even a bird perching on the branches could sometimes lead to damaged leaves dropping prematurely (pers. obs.). It also led to a reduction in plant height, and growth rate of the Whitney Farm test treatment plants compared to the control treatment.

Even more impressive at Whitney Farm is the effect that *F. intermedia* feeding damage has had on plant growth beneath lantana bushes over the two-year period. The test treatment recorded significantly greater grass, herbaceous and creeper cover at the test treatment. The initial response to insect feeding damage at the test treatment was reproductive, expressed as an increase in the number of seeds and flowers. Such measures in the face of relentless feeding damage such as experienced by the Whitney Farm lantana variety can only be temporary, as the plant can not completely cease normal physiological processes by redirecting energy (Van der Meijden 1989). This gives plants underneath and around lantana bushes a window period to receive more sunlight and allows them to effectively photosynthesise and compete with the weed.

The mirid *F. intermedia* has shown some promise as a biological control agent able to control lantana in only one of the five sites. It has great potential in climatically suitable release sites such as Whitney Farm and even East London. Climatic suitability evaluations of potential release sites must be made priority before release are made. Use of climatic modelling computer programs such as the principal component analysis (PCA) based technique described by Robertson *et al.* (2001) are useful in this regard, even though these may have limitations in the quality of data used and some in predicting microclimatic changes. Further research should also focus on the acquisition of a cold-adapted strain of *F. intermedia* for sites such as Heather Glen that do not drop 100% of their leaves over the cooler months. Such a strain should be able to survive harsh conditions and continue to affect the remaining lantana leaves through the winter, placing added pressure on the weed itself. The mirid also has a great ability to disperse to surrounding trees, dispersing by as much as 20-25m over the course of the field trials in the East London site, and to surrounding trees in Whitney Farm (pers. obs.). This spread may be part of the explanation for non-detection of insects at East London, but more importantly, it shows that at population peaks, the insects can locate and fly to potential hosts in the locality of congregated thickets of lantana. The quick movement on the leaves, along with flight, enables the insect to fly away from potential predators, making it less vulnerable to predation than more sluggish insects such as *T. scrupulosa* that were reported to be under some degree of predation (Broughton 2000).

The changes in the internode lengths means due to changing the measuring techniques that were experienced by the test treatment at Whitney Farm are very odd (from a mean of 30.88cm to 39.05cm), and raises a question about the compatibility of the two techniques, and the effectiveness of the second technique, particularly in comparing internode length. The continuous removal of branches at the destructive sample trees may perhaps have triggered growth of branches and internodes over the one-year period. This in turn could have led to the increase in internode lengths recorded as a trend at all the sites. Use of technique 1 to measure damage may also have resulted in overestimation of damage during the initial period (February – September 2002). The monthly recordings of damage at the same five leaf pairs made using technique 1 resulted in the possibility of damage made in one month being recorded in another month, such as seen by the almost similar amount of damage at Heather Glen and Whitney Farm, despite the mirid going extinct at the former . In the process of recording the data in the field, it was impossible to differentiate damage made in one particular month from that made in another. Had technique 1 been used throughout, then damage at East London and at Whitney Farm in particular, would have been a great deal more due to these repetitive measurements.

Even though care was taken to choose controls that were nearby and similar in character to the test treatments, it is however possible that the control and test sites at any or all the sites did not have identical growing conditions. The amount of light, water, disturbance to the plant received may have varied under field condition, creating pseudo-replication effect. Therefore care should be taken in interpreting the results. Another point to note is on plant height measurement. Plant height, indicating vertical and linear growth, may be inadequate by itself in determining overall growth of lantana and the impact of a biological control agent on the overall growth of lantana. This is because growth of *L. camara* branches can be non-directional and may be in any orientation on and around the plant. Plant height measure by itself (as in technique 2) only gives us one dimension of this total growth, but is more effective in giving a fuller growth result when measured in combination with the branch length (as in technique 1).

Chapter 4

General Discussion

Preface

In this chapter the major findings of the laboratory and field studies and their meaning within the Eastern Cape context are integrated and discussed in relation to three major factors identified as major barriers to the establishment and effectiveness of *F. intermedia* on *L. camara*, both from this study and from reviewed literature. Areas needing further study are highlighted and ways to improve the success of the current and future releases explored.

4.1 Introduction

The biological control programme against *Lantana camara* (Verbenaceae) in South Africa has been extensive and about 21 species of biological control agents have been released (Julien and Griffith 1998). However, only 11 of these agents have established, and three of these are considered to be the most efficacious in the country (Baars 2002). Some success may have been achieved (Cilliers and Neser 1991), but this is not easy to quantify. There has been renewed emphasis on supplementing the biological control programme with additional agents. The establishment of the released agent *F. intermedia* (Hemiptera: Miridae) at two sites in the Eastern Cape sites is thus good news to the programme in the country. However, three factors are suggested as being most influential in the lack of establishment and reduced control by this biological control agent on *L. camara* in the field studies conducted. These are adverse climatic conditions, lantana varietal preference by *F. intermedia*, and inadequate numbers of individuals released. These factors are discussed in this section and recommendations to allow for improved success in future releases in the Eastern Cape are explored.

4.2 Effects of climatic conditions

Falconia intermedia established on two of the three coastal sites, Whitney Farm and East London, where releases were made (Chapter 3). This suggests that the Eastern Cape coastal sites, with moister and warmer conditions and with lantana sites that maintain most of their leaves through the year, are more suitable for releases of the mirid than inland sites. Further results from data loggers at Heather Glen farm suggest that *F. intermedia* individuals released at this site failed to establish due to significantly colder climatic conditions. This agent performed well on the Heather Glen farm (WP EC3) variety in laboratory trials where climatic conditions were controlled, showing that this variety was suitable for oviposition (Chapter 2). This site experienced harsh winter conditions during the field trials, resulting in a number of leaf drops during this period. Similar reports have been made in reviews by Day and Neser (2000) and Broughton (2000). Climatic conditions were been singled out as the most important factor in the establishment and control by biological control agents in these reviews. Adverse climatic conditions may act directly on the phenology of released agents by slowing vital physiological processes, as well as indirectly by changing the plant-insect interaction (Baars 2002). Low temperatures have also been reported to reduce the potential rate of population growth in some insects (Harley *et al.* 1979, Cilliers and Neser 1991), leading to an increase in insect mortalities. Insects may also become inactive due to low temperatures, increasing the chances of predators preying on them (Day *et al.* 2003).

The above-mentioned factors make it unlikely that the current strain of *F. intermedia* will establish and effect meaningful pressure on lantana if released in areas with harsh winter conditions such as Heather Glen farm. Suitable year-round climatic conditions, such as those experienced in the warm and moist subtropical areas of South Africa and the coastal regions in the Eastern Cape, are vital for the success of leaf-feeding insects. Having said that, acquiring a cold-adapted biotype of the highly fecund and effective *F. intermedia* in the native range may be worth investigating. Releases made from larger samples and from climatically different areas in the native ranges may increase the genetic variation in the naturalised range. This may possibly enhance the ability of the mirid to acclimatise (Day *et al.* 2003), which may lead to better establishment and control in sites such as Heather Glen farm.

Alternatively, strains of promising leaf-feeding agents with over-wintering mechanisms such as diapause, should be prioritised for release in areas with severe winter conditions where plants are under little stress from biological control agents. These mechanisms allow agents to have higher survival rates over the winter months and then to impact the lantana early in the growing season before the plants have recovered from the previous summer's damage. Populations persisting in low numbers at East London are most likely due to cooler temperatures over the 2003 winter season. The feeding impact at this site may be increased by supplementing the population numbers with individuals from sources such as insectaries, and sites where the mirid has established (e.g. Whitney Farm).

Modelling techniques such as the PCA-based technique by Robertson *et al.* (2001), FloraMap (Jones and Gladkov 1999), and Biomapper (Hirzel *et al.* 2001a) modelling packages are useful as they are used to generate maps predicting potential establishment and spread of invasive species in the introduced range. These techniques predict the most climatically suitable sites in the introduced range of agents, and should allow for more informed releases according to the needs of biological control agents such as leaf-feeding insects. These technique are mostly limited by the quality of data they are given. Knowing and closely matching the microclimatic conditions of potential release sites with those of the collection sites in the native range, and using this information in conjunction with the general predicted suitable sites by modelling techniques, may possibly increase chances of establishment at release sites. Techniques may also be helpful in the redistribution of agents already established, as well as predicting the potential distribution of new agents in early stages after releases. However, the techniques do not in themselves guarantee successful control of weeds at a particular site, as a number of other factors such as predation, parasitism and varietal preference, may come into play to prevent establishment or effective control of the weed.

4.3 Varietal Preference

A long process of man-mediated hybridisation (Stirton 1977) and selection has created an enormously variable genetic complex that is *L. camara*. This factor, along with further hybridisation in the field (Spies and Stirton 1982a, b, c), causes this polyploid complex to be a challenging target weed for biological control. *Lantana camara* varieties in the native ranges are rarely morphologically similar to the lantana varieties in the invaded ranges (Smith and Smith 1982). This creates a possibility that agents released on *L. camara* varieties may not establish or perform well. Indeed a number of authors have reported varietal preference in studies they have conducted (Haseler 1966, Harley 1973, Cilliers and Neser 1991, Broughton 1999, Urban and Simelane 1999, Day and Neser 2000).

In the laboratory trials conducted, *F. intermedia* seemed to indicate no major varietal preference for any of the five Eastern Cape *L. camara* varieties tested (Chapter 2). The results seem to suggest that the mirid released would perform best in field trials on two of the varieties, Whitney Farm (WP EC2) and Heather Glen farm (WP EC3), but also that the mirid released on the other three Eastern Cape sites would perform comparatively well. However, in field releases establishment was only achieved in only two of these sites, Whitney Farm and East London, with good performance at the Whitney Farm and reasonable performance at East London. At two sites, Port Alfred and Lyndhurst farm, the morphological characteristics of the varieties were different between field and laboratory trials. The leaves of these two varieties were tougher, smaller and darker in colour in field trials compared to the leaves in the laboratory cultures. As the mirid is a leaf-feeder, such differences may have contributed to non-preference of these varieties, and possibly to non-establishment.

Possible reasons for the differences in variety may be due to soil quality and climatic variability. Plants in the laboratory studies were reared and maintained on a potting mixture providing them with fertile soil. The soil in the pots was also fertilised regularly to ensuring that plants received sufficient nutrients. This kind of action was not replicated in the field release sites and may have lead to inferior plant quality in field plants compared to the laboratory plants. Less healthy plants may lack sufficient nutrients that are vital for oviposition and the complete development of the young mirids (Day *et al.* 2003).

Falconia intermedia releases have been made on a few varieties in the Eastern Cape in this study. Despite the white-pink variety being one of the common varieties in the Eastern Cape, there are other common varieties on which releases have not been made, or where results from past releases have not been published. The results from this study indicate that releases of this agent in climatically suitable and multivariate areas in the Eastern Cape should offer some level of success as this insect had no clear preference for any of the varieties on which it was released in laboratory conditions. This study seems to agree with the findings by Baars (2002) that this agent does not exhibit varietal preference under laboratory conditions.

4.4 Number of individuals released

Observations made from insects released at both laboratory and field trials are that there was an initial period where the insect populations recorded some mortalities. This may be due to the fact that insects were reared on certain varieties and then released on others. Individuals in the populations may differ in their genetic ability to feed on different varieties after experience with one variety. In field trials other factors such as predation may also have had an effect. Differences in climatic conditions, as described in the above sections, may also have had a negative effect on the populations, as insects released at these Eastern Cape sites were reared from farms where climatic conditions were more favourable for mirid survival. To offset these initial setbacks it is necessary that releases of *F. intermedia* be made in much higher numbers to increase chances of establishment. This may also be helpful in accelerating the time it takes for populations to be increased, as mates are more accessible for insect reproduction.

4.5 Conclusion

It has been acknowledged that a suite of natural enemies would increase the chances of the lantana biological control programme (Oosthuizen 1964, Cilliers 1983, 1987a). In a survey by Baars (2002) it was discovered that there were three non-lepidopteron biological control agents, *C. lantanae*, *O. lantanae*, and *T. scrupulosa* established in the Eastern Cape. Three introduced lepidopteron species, *S. haemorrhoidalis*, *E. lantana*, and *L. pusillidactyla* have also established. However, all these agents had occasional abundance while their impact is minimal. This means that there is insufficient pressure on the *L. camara* varieties in the Eastern Cape as agents such as *O. scabripennis* and *U. girardi* are absent here. Therefore more releases of the mirid, as well as other promising agents, should be made in climatically suitable areas of the Eastern Cape. Redistribution of other agents to the Eastern Cape varieties should also be considered to bolster the *L. camara* programme.

References

Baars, J-R., 2000. Emphasizing behavioural host-range: the key to resolving ambiguous host-specificity results on *Lantana Camara* L. In: Spencer, N.R. (Ed), Proceedings of the X International Symposium on Biological Control of Weeds, Bozeman State University, USA, pp. 887-896.

Baars, J-R., 2002. The life and host specificity of *Teleonemia vulgate* (Hemiptera: Tingidae), a potential biocontrol agent of *Lantana Camara* (Verbenaceae). African Entomology. 10: pp. 315-324.

Baars, J-R., 2002. Biological control initiatives against *Lantana camara* L. (Verbenaceae) in South Africa: an assessment of the present status of the programme, and an evaluation of *Coelocephalion camarae* Kissinger (Coleoptera: Brentidae) and *Falconia intermedia* Distant (Heteroptera: Miridae), two new candidates natural enemies for release on the weed. PhD thesis. Department of Zoology and Entomology. Rhodes University, South Africa.

Baars, J-R. and 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). African Entomology Memoir, 1: pp. 21-33.

Baars, J-R., Urban, A.J. and Hill, M.P. 2003. Biology, host range, and risk assessment supporting release of *Falconia intermedia* (Heteroptera: Miridae), a new biocontrol agent for *Lantana camara*. Biological Control. pp. 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 Science and Technology 6: pp. 251-261.

Briese D.T. 2000. Impact of the *Onopordum capitulum* weevil *Larinus latus* on seed production by its host-plant. Journal of Applied Ecology. 37: pp. 238-246.

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

Broughton, S. 2000a. Review and evaluation of lantana biocontrol programs. Biological Control. 17: pp. 272-286.

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

Cilliers, C.J. 1987a. Notes on the biology of the established insect natural enemies of *Lantana camara* L. (Verbenaceae) and their seasonal history in South Africa. Journal of the Entomological Society of Southern Africa 50: pp. 1-13.

Cilliers, C.J. 1987b. The evaluation of three insect natural enemies for biological control of the weed *Lantana camara* L. Journal of the Entomological Society of Southern Africa 50: pp. 15-34.

Cilliers, C.J. and Neser, S., 1991. Biological control of *Lantana camara (*Verbenaceae) in South Africa. Agricultural Ecosystem Environment 37: pp. 57-75.

Crawley, M.J. 1986. The population biology of invaders. Philosophical Transactions of the Royal Society of London, B. Biological Sciences 314: pp. 711-731.

Crawley, M.J. 1989. Insect herbivores and plant population dynamics. Annual Review of Entomology 34: pp. 531-564

Day, M.D. and Neser, S. 2000. Factors influencing the biological control of *Lantana camara* in Australia and South Africa. In: N.R. Spencer (ed.). Proceedings of the X International Symposium on Biological Control of Weeds, Bozeman, Montana: pp. 897-908.

Day, M.D., Wiley, C.J., Playford, J. and Zalucki, P.M. 2003. Lantana: current management status and future prospects. Australian Centre for International Agricultural Research, Canberra. Monograph 102.

Everist, S.L. 1981. Poisonous Plants of Australia. 2nd edn. Angus and Robertson, Sydney.

Gassman, A. and Schroeder, D. 1995. The search for effective biological control agents in Europe: history and lessons from leafy spurge (*Euphorbia esula* L.) and cypress spurge (*Euphorbia cyparisias* L.). Biological Control 5: pp. 466-477.

Gentle, C.B. and Duggin, J.A. 1997a. Allelopathy as a competitive strategy in persistent thickets of *Lantana camara* L. in three Australian forest communities. Plant Ecology. 132: pp. 85-95.

Graaff, J.L. 1986. *Lantana camara*, the plant and some methods for its control. South African Forestry Journal 136: pp. 26-30.

Graaff, J.L. 1987. The seed-fly *Ophiomyia lantanae* and other factors responsible for reducing germination in *Lantana camara* forms found in Natal. South African Journal of Botany 53: pp. 104-107.

Harley, K.L.S, 1971. Biological control of *Lantana.* PANS (C) 17: pp. 433-437.

Harley, K.L.S. 1973. Biological control of *Lantana* in Australia. In: A.J. Wapshere (ed.). Proceedings of the III International Symposium on Biological Control of Weeds Montpellier, France: pp. 23-29.

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

Harris, P. and McEvoy, P. 1995. The predictability of insect host plant utilisation from feeding tests and suggested improvements for screening weed biological control agents. In: E.S. Delfosse and R.R. Scott (eds.). Proceedings of the VIIIth International Symposium on Biological Control of Weeds. 2-7 February 1992, Canterbury, New Zealand. Lincoln University. DSIR/CSIRO, Melbourne, pp. 125-131.

Harris, P. and Zwolfer, H. 1968. Screening of phytophagous insects for biological control of weeds. Canadian Entomology 100: pp. 295-303.

Haseler, W.H. 1966. The status of insects introduced for biological control of weeds in Queensland. Journal of the Entomological Society of Queensland 5: pp. 1-4.

Henderson, L. 2001. Alien Weeds and Invasive Plants, Handbook 12. Agricultural Research Council, Plant Protection Research Institute, Pretoria.

Herzil, A. H., Hausser, J. and Perrin, N. 2001a. Biomapper 1.0. Lausanne, Laboratory for Conservation Biology, URL: http://www.unil.ch/biomapper

Hill, M. P., Center, T.D., Stanley, J.N., Cordo, H.A., Coetzee, J. and Byrne, M. J. 2000. The performance of the water hyacinth mirid, *Eccritotarsus catarinensis*, on water hyacinth and pickerelweed: a comparison of laboratory and field results. In: N.R. Spencer (ed.). Biological Control of Weeds in South Africa (1990-1998). African Memoir 1: pp. 81-88.

Holm, L. G., Plucknett, D.L., Pancho, J.V. and Herberger, J.P. 1977. The world's worst weeds. The University Press of Hawaii, Honolulu.

Hokkanen, H. and Pimentel, D. 1984. New approach for selecting biological control agents. *The Canadian Entomologist.* 116: pp. 1109-1121.

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

Julien, M.H. and Griffiths, M.W. 1998. Biological Control of Weeds. A World Catalogue of Agents and their Target Weeds, Fourth Edition. CABI Publishing, Wallingford, UK.

Kellerman, T.S., Naude, T.W. and Fourie, N., 1996. The distribution, diagnoses, and estimated economic impact of plant poisonings and mycotoxicoses in South Africa. Onderstepoort Vetenarian Research 63: pp. 65-90.

Marais, C., van Wilgen, B.W. and Stevens, D. 2004. The clearing of invasive alien plants in South Africa: a preliminary assessment of costs and progress. South African Journal of Science 100: pp. 97-103.

Marohasy, J. 1998. The design and interpretation of host-specificity tests for weed biological with particular reference to insect behaviour. Biocontrol News and Information 19: pp. 13-20.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. Oikos 40: pp. 329-336.

McNaughton, S. J. 1986. On plants and herbivores. American Nature 128: pp. 765-770.

Morton, J.F., 1994. Lantana, or red sage (*Lantana camara L.*[Verbenaceae]), notorious weed and popular garden flower; some cases of poisoning in Florida. Economic Botany 48: pp. 259-270.

Muniappan, R. 1988. Biological control of the weed, *Lantana camara* in Guam. Journal of Plant Protection in the Tropics 5: pp. 99-101.

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

Munir, A.A. 1996. A taxonomic review of *Lantana camara* L. and *L. montevidensis* (Spreng.) Briq. (Verbenaceae) in Australia. Journal of the Adelaide Botanical Gardens 17: pp. 1-27.

Neser, S. and Cilliers, C.J., 1990. Work towards biological control of *Lantana camara*: perspectives. In: Delfosse, E.S. (Ed.), Proceeding of the VII International symposium on Biological Control of Weeds, IST. Sper. Patol. Veg. (MAF), Rome, pp. 363-369.

Oosthuizen, M.J. 1964. The biological control of *Lantana camara* L. in Natal. Journal of Entomological Society of Southern Africa. 27: pp. 3-16.

Palmer, W.A., and Pullen, K.R., 1998. The host range of *Falconia intermedia* (Distant) (Hemiptera: Miridae): a potential biological control agent for *Lantana camara* L. (Verbenaceae). Proceedings of the Entomological Society Washington 100: pp. 633-635.

Papaj, D.R. and Rausher, M.D. 1983. Individual variation in host location by phytophagous insects. In: S. Ahmad (ed.). Herbivorous Insects. Host-seeking Behaviour and Mechanisms, Academic Press, New York: pp. 77-124.

Perkins, R.C.L. and Swezey, O.H. The introduction into Hawaii of insects that attack lantana. Bulletin of the Experiment Station of the Hawaiian Sugar Planters' Association 16: pp. 1-83.

Pinhey, E.C.G. 1975. Moths of Southern Africa. Tafelberg, Cape Town.

Radunz, L.A.J. 1971. Some aspects of the preferential behaviour of *Teleonemia scrupulosa Stål,* towards its host plant *Lantana Camara.* Honours thesis, Department of entomology, University of Queensland, Brisbane, 53pp.

Robertson, M.P., Caithness, N. and Villet M.H. 2001. A PCA-based modelling technique for predicting environmental suitability for organisms from presence records. Diversity and Distributions 7: pp. 15-27.

Sanders, R.W. 1989. *Lantana* sect *camara* (Verbenaceae) in Hispaniola: novelties and notes. Moscosoa 5: pp. 202-215.

Sands, D.P.A. & Harley K.L.S. 1980. Importance of geographic variation in agents selected for biological control of weeds. In: Proceedings of the V International Symposium on Biological Control of Weeds (ed. Del Fosse, E.S.), Brisbane, Australia: pp. 81-89.

Scott, L.J. 1998. *Identification of Lantana spp.* Taxa in Australia and the South Pacific. Final Report to ACIAR, Cooperative Research Centre for Tropical Pest Management, Brisbane, Australia.

Seawright, A.A. 1963. Studies on experimental intoxication of sheep with *Lantana camara.* Australian Veterinary Journal 39: 340-344.

Smith, L.S. and Smith, D.A., 1982. The naturalised *Lantana camara* complex in eastern Australia. Queensland Botanical Bulletin No. 1. Queensland Department of Primary Industry, Brisbane.

Spies, J.J. 1984. A cytotaxonomic study of *Lantana Camara* (Verbenaceae) from South Africa. South African Journal of Botany 3: 231-250.

Spies, J.J., and Du Plessis, H. 1987. Sterile *Lantana camara*: fact or theory. South African Journal of Plant Soil 4: pp. 171-174.

Spies, J.J. and Stirton, H. 1982a. Chromosome numbers of the South African plants. South African Journal of Botany 48: pp. 21-22.

Spies, J.J. and Stirton, H. 1982b. Meiotic studies of some South African cultivars of *Lantana camara*. Bothalia 14: pp. 101-111.

Spies, J.J. and Stirton, H. 1982c. Embryo sac development in some South African cultivars of *Lantana camara*. Bothalia 14: pp. 113-117.

Stirton, C.H., 1977. Some thoughts on the polyploidy complex *Lantana camara* L. (Verbenaceae). In: Proceedings of the Second National Weeds Conference of South Africa. A.A, Balkema, Cape Town, 99: pp. 321-344.

Stirton, C.H., and Erasmus, D. 1990. The naturalised *Lantana camara* L. complex in Natal. Unpublished report. 6 pp.

Sutherst, R.W., Maywald, G.F., Yonow, T. and Stevens, P.M. 1999. CLIMEX: Predicting the effects of climate on plants and animals, Version 1.1. CSIRO, Melbourne.

Swarbrick, J.T., Wilson, B.W. and Hannah-Jones, M.A. 1995. The biology of Australian weeds: *Lantana camara* L. Plant Protection Quarterly 10: pp. 82-95.

Swezey, O.H. 1924. Present status of lantana and its introduced insect enemies. In: The introduction into Hawaii of insects that attack lantana (eds. Perkins, R.C.L. & Swezey, O.H), Bulletin of the Experiment Station of the Hawaiian Sugar Planters' Association 16: pp. 1-83.

Urban, A.J. & Simelane, D.O. 1999. Performance of a candidate biological agent, *Falconia intermedia* (Hemiptera: Miridae), on selected biotypes of Lantana camara (Verbenaceae). In: Van Rensburg, J.B.J. & J. van den Berg (eds.). Proceedings of the Twelfth Entomological Congress, Potchefstroom, South Africa: 120.

Van der Meijden, E. W. M. and Verkaar., H. J. 1989. Defence and regrowth, alternative strategies in the struggle against herbivores. Oikos 51: pp. 355- 363.

Versfeld, D.B., Le Maitre, D.C. and Chapman, R.A. 1998. Alien invading plants and water resources in South Africa. Water Research Commission Report No. 748/1/97.

Wan, F. and Harris, P. 1997. use of risk analysis for screening weed biological control agents: *Altica carduorum* Guer. (Coleoptera: Chrysomelidae) from China as a biological control agent of *Cirsium arvense* (L.) in North America. Biocontrol Science and Technology 7: pp. 299-308.

Wapshere, A.J. 1970. The effect of human intervention on the distribution and abundance of *Chondrilla juncea* L. In: Proceedings of the Advanced Study Institute on 'Dynamics of Numbers in Populations' (eds. Den Boer, P.J. & Gradwell), Oosterbeek, the Netherlands: pp. 469-477.

Williams, H. 2003. The suitability of *Alagoasa extrema* Jacoby (Coleoptera: Chrysomelidae: Alticinae), as a biological control agent for *Lantana camara* L. in South Africa. MSc thesis. Department of Zoology and Entomology. Rhodes University, South Africa.

Winder, J.A. 1980. Factors affecting the growth of lantana in Brazil. PhD thesis, Department of Agriculture and Horticulture, University of Reading, UK.

Winder, J.A. 1982. *Ophiomyia lantanae* (Diptera: Agromyzidae) and associated parasitoids emerging from *Lantana* spp. Fruits (Verbenaceae) in Parana state, Brazil. Revista Brasileira de Biologia 42: pp. 647-652.

Winder, J.A &K.L.S. Harley. 1983. The phytophagous insects on *Lantana* in Brazil and their potential for biological control in Australia. Tropical Pest Management 29: pp. 346-362.

Withers, T.M. 1997. Changes in plant attack over time in no-choice tests: an indicator of specificity. In: Proceedings of the Fiftieth New Zealand Plant Protection Society Conference, 18-21 August 1997, Canterbury, New Zealand, pp. 214-217.

Zwölfer, H. and Harris, P. 1971. Host specificity determination of insects for biological control of weeds. Annual Review of Entomology 16: pp. 159-178.