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AN EVALUATION OF THE EFFECTS OF IMPORTED INSECTS ON THE WEED *LANTANA CAMARA* L. IN SOUTH AFRICA.

by

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CONTENTS

Lantana camara L. (Verbenaceae) : Tip of branch, flowers and seed-heads (with berries).

1. RÉSUMÉ

The plant, Lantana camara L. (Verbenaceae), is a weed in tropical and subtropical areas around the world. In many countries, including South Africa, biological control of this weed has been attempted.

Although 12 insect species have been imported into South Africa, only four species established and these are dealt with in this study. Ophiomyia lantanae Diptera: Agromyzidae) a seed fly, is briefly dealt with; the main emphasis is on the leaf damaging species Teleonemia scrupulosa Stål (Hemiptera: Tingidae) and two leaf mining beetles, Octotoma scabripennis Guérin and Uroplata girardi Pic. (Hispidae: Coleoptera).

In evaluating the insect damage to lantana leaves, monthly samples of branches were taken over three seasons from 1977-80. This destructive sampling allowed the study of population build-up of the insects. In addition, counts were made of the numbers of damaged and healthy leaves, flowers and seeds and the damage related to the activities of the different stages of the hispids and the tingid.

Insect exclusion experiments were also used to determine the effect of the insects on the growth of L. camara.

The results reported in this thesis clearly indicate that the imported natural enemies retard L. camara growth and vigour and the effects are manifested in a marked reduction in stem diameter, internodal length, leaf size, leaf lifespan and in flower and seed set.

2. INTRODUCTION

Characteristics of the plant

The genus Lantana is mainly a New World genus of about 150 species, known mostly from tropical America. Marr (1962), Everist (1974), and Stirton (1978) describe Lantana camara L. as a compact bushy shrub or semi-scrambler. The many branches are square in cross section with backwardly curved prickles along the angles, or in some forms nearly devoid of prickles but with stiff hairs. The opposite leaves are usually lanceolate to obovate, each pair set at right angles to the pair above. Leaves are abruptly narrowed at the base into a slender stalk and less abruptly tapered at the apex to a blunt drawn-out tip (see frontispiece). In most forms the leaves are more or less flat or the edges are slightly curved downward. The thick, rough, finely hairy, dark-green foliage smells strongly when crushed. When a set of leaves matures, side shoots are put out, and these side shoots represent most of the new growth. The compact flower heads (see frontispiece), each containing up to forty flowers, are flat-topped or slightly rounded and are borne in the axils of the upper leaves. Each tubular flower has four more or less equal lobes, the colour changing with age. The flowers in each head open successively from the outside inward. Forms with pink, red, white, orange, crimson and yellow flowers are know. Berries are green at first, dark bluish to black at maturity, with a hard "stone" divided into two one-celled pyrenes that contain two seeds. The fruits are borne in clusters of up to thirty.

The genus Lantana in South Africa

There are three indigenous species of Lantana in South Africa, of which the most widespread is L. rugosa Thunb., while L.trifolii L. and L. mearnsii Moldenke are restricted to the Transvaal (Phillips, 1951; Stirton, 1977). Two exotic species have become naturalized in the Republic: L. montividensis Sprengel and L. camara.

L. montividensis is a trailing species lacking prickles and has rose-lilac to purplish-pink flowers. A white-flowered form is also known. This species originates from Montevideo, Uruguay (Howard, 1970), and has not attained weed status in South Africa. L. camara, with which this study is concerned, occurs as a native shrub on islands of the West Indies, Central America, Mexico and South America (Howard, 1970) and has become a noxious weed in South Africa. The first records of its introduction into the country are dated 1858, when it was introduced into Cape Town, and 1883, when it was introduced into Natal (Stirton, 1977). The Lantana species introduced in these early times came from Europe and Mauritius and had various species names, but L. camara was among them (Stirton, 1977). The many forms of L. camara are separated on the basis of size, shape and colour of the flowers, size, colour and hairiness of the leaves and prickles on the stem.

Lantana camara as a problem plant

L. camara as we know it today is a cosmopolitan weed in the tropical and subtropical regions of the world. Forty-seven countries have reported it as a weed (Holm et al., 1977). Leaves and seeds of the plant are poisonous to livestock, the poisonous substances being almost certainly a triterpene (Louw, 1943; 1948; Watt & Breyer-Brandwÿk 1962; Seawright, 1965; Everist, 1974). Humans, are known to have died from neuro-circulatory collapse (Stirton, 1978) after eating the berries. Not all forms of L. camara are toxic (Seawright, 1965; Everist, 1974). L. camara is also a problem because of its thicket-forming habit and vigorous growth, which enable it to invade veld, forests and riverbanks. In any botanically disturbed situation it quickly forms dense thickets (Fig. 1).

Fig. 1. Lantana camara thicket.

In 1910, Wood reported L. camara to be firmly established in the Natal coastal districts. In 1922, in correspondence with the Natal Provincial Secretary, it was stated that L. camara invaded neglected or derelict lands and natural bush, and that it was not uncommon to find impenetrable half-acre patches. In view of its bad record in other coutries, the Division of Agriculture in 1922 suggested the proclamation of L. camara as a noxious weed. It was proclaimed as a weed in 1946 in the Province of Natal (Act No. 42 of 1937, Proclamation 167 of 1946). By 1943, Louw had proved that L. camara is poisonous to cattle, and this probably led to Declaration No. 38 of 1954 declaring it a weed throughout South Africa.

The problem of L. camara, therefore, is not only that it is poisonous to stock, but also that it invades both plantations and natural bush. The coastal bush, near Durban, is a typical example of an area where L. camara is so vigorous that it tends to crowd out the indigenous flora. The same applies to the Barberton-Nelspruit and Tzaneen areas. Stirton (1978) points out that in the Cape, as in other parts of South Africa, it inhabits fields, orchards, hillsides, waste ground, overgrazed or burnt veld, forest margins, plantations and natural forests. By suppressing natural vegetation it reduces the carrying capacity and value of the veld. In plantations, L. camara can grow in shade, though it is then somewhat etiolated; but once the trees are cut down, it grows vigorously and forms an impenetrable thicket (Birch, 1961). Wherever soil or vegetation is disturbed, by fire or overgrazing, L. camara soon develops a dense stand. Invasion by L. camara is also accompanied by increased surface runoff, and the footpaths which cattle are forced to make between the plants eventually lead to soil erosion. It is known that in dense stands of L. camara the capacity of the soil to absorb heavy rain is lower than under good grass cover (Birch, 1961).

Area infested by Lantana camara

The most recent distribution of L. camara in southern Africa was drawn up by Stirton in 1977. The main infestations in South Africa (Fig. 2, Table 1) occur along the eastern coast and in the Transvaal Lowveld. It seldom occurs in areas where temperatures frequently fall below 5°C. Other limiting factors are rainfall, surface temperature and altitude.

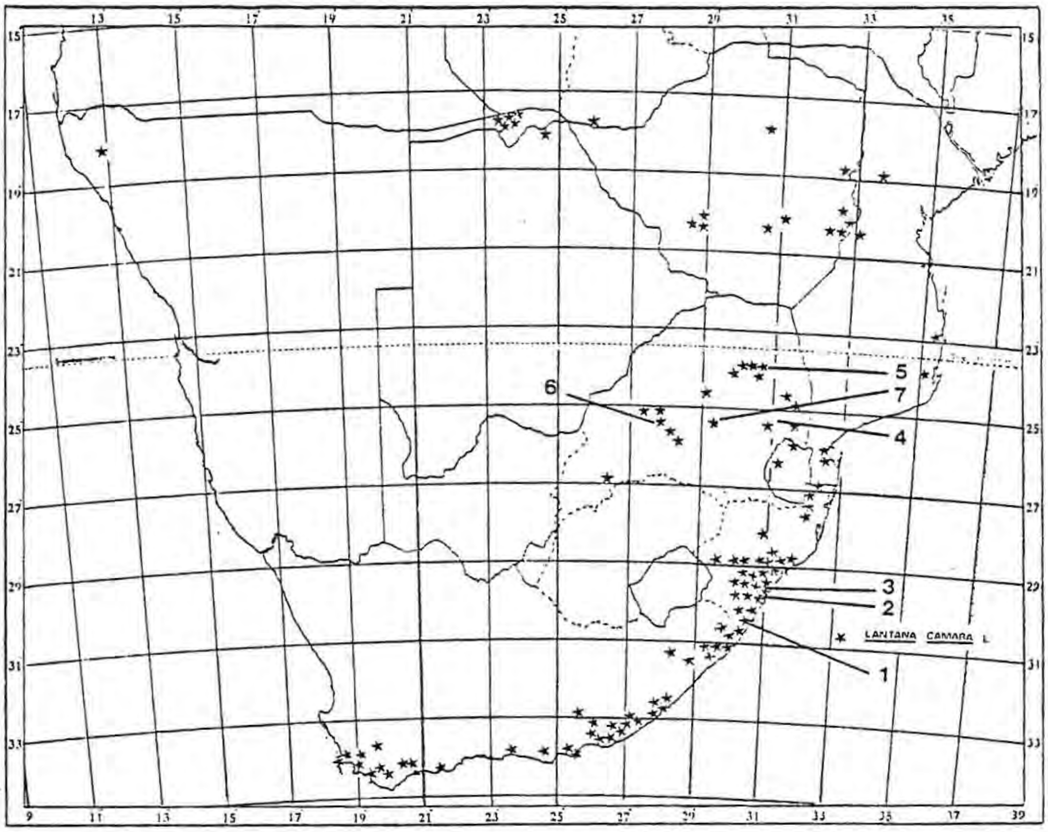

Fig.2. The present distribution of Lantana camara L. in southern Africa. (After Stirton, 1977). Study areas:
1. Margate, 2. La Mercy, 3. Shakaskraal, 4. Nelspruit & Burgers Hall, 5. Tzaneen (Letaba), 6. Buffelspoort, 7. Pretoria.

Table 1: Area infested by Lantana camara in South Africa.

Year	Region	Hectares	Source
1950	Natal	8 274	du Toit (1950)
1962	Natal	24 423	Marr (1962)
1962	Tvl. Lowveld	2 744	Marr (1962)
1962	E. Cape (Albany/ Bathurst)	1 168	Marr (1962)
1976	Tvl. Lowveld	13 300	Smith (1976)
1977	E. Cape Coast	?	Stirton (1978)
1981	Estimated Total	52 000+	This study

Table 1 shows that in Natal the area infested increased about 3-fold in the 12 years from 1962 to 1976 and that from 1962 to 1976 it increased about 5-fold in the Transvaal Lowveld. The absence of the plant as a weed in the Orange Free State, though it occurs in gardens (Marr, 1962), is due to the fact that the area is climatically unfavourable to this subtropical plant.

Attempts to control Lantana camara

Chemical Control

Several herbicides are registered for use against L. camara in South Africa (Hattingh & Swanepoel, 1980). All herbicides are most effective when used on actively growing plants in late spring or early summer. Picloram (potassium salt) is effective as a leaf or stem spray, to be repeated on regrowth. Dicamba + 2,4,5 - T is used as a stem treatment, and on slashed plants 2,4,5 - T (butyl-isobutyl-ester) is applied. Picloram + 2,4,5 - T (amine) or glyphosate is effective as a cover spray. L. camara regrows vigorously after herbicide treatment, and regrowth should be sprayed. These follow-up operations together with the cost of labour and herbicides make chemical control expensive. Even so, it is not always successful, and a combination of chemical and mechanical control is usually needed to eradicate L. camara.

Mechanical Control

Seedlings and small plants can be uprooted by hand. Established, thick-stemmed plants over one metre high can be effectively removed by attaching to a tractor several unequal lengths of chains or cables, which are looped round the bushes and the bushes then pulled out. A hand leverage tool, such as the Mandy Pick, is practicable and preferable for extracting bushes in difficult terrain such as steep slopes, riverbanks or gullies. All slashed or extracted plants should immediately be stacked, allowed to dry, and burnt (Haigh et al., 1976 ; Duthoit, 1977). Reclaimed land, if not immediately cultivated, should be planted to

Panicum maximum Jacq. (guinea grass) or Chloris gayana Kunth. (Rhodes grass) to prevent re-establishment of L. camara from seedlings. On no account should slashed plants be left in place, as this results in even denser thickets (Pamphlet E. 8.1.1/1981, Farming in South Africa). With the increasing cost of labour, fuel and the often difficult terrain infested with L. camara, the third alternative control method, biological control, becomes increasingly more attractive.

Biological Control

In 1952 the Natal Agricultural Region suggested to the then Division of Entomology that the biological control of L. camara be investigated. Such a project was suggested in 1959 by Dr E.C.G. Bedford after a visit by Dr F.J. Simmonds, Director, C.I.B.C. to South Aftica. In 1960 funds were made available for three years. In those years the following insects were imported: Ophiomyia lantanae (Frogg.) (Diptera: Agromyzidae), Hypena strigata Fab. (Lepidoptera: Noctuidae), Anania haemorrhoidalis (Guen) (formerly Syngamia haemorrhoidalis Guen) (Lepidoptera: Pyralidae), Neogalea esula (Druce) (Lepidoptera: Noctuidae) and Teleonemia scrupulosa Stål (Hemiptera: Tingidae) (Oosthuizen, 1964). T. scrupulosa and O. lantanae became established, throughout South Africa, and are dealt with in this thesis.

One of the three Lepidoptera imported, H. strigata (misidentified as H. jussalis), is indigenous to Africa. Anania haemorrhoidalis could not be mass-reared, and the attempt to establish it met with failure. C. esula was released but did not become established, and laboratory cultures were wiped out by an unknown disease (Oosthuizen, 1964; Cilliers, 1977). Before the project was suspended in 1964, Oosthuizen (1964) made a survey of insects on L. camara and concluded that none of the indigenous species was capable of doing much damage to the plant, since most of the insects he found were not plant feeders.

After a visit by the late Dr D.P. Annecke to Australia in 1967, and because of the promising work undertaken there, the lantana biological control project in South Africa was re-started at the end of 1968. In close collaboration with, and leaning heavily on advice from Dr K.L.S. Harley, CSIRO, Brisbane, Messrs Bill Haseler and Brian Willson, Department of Lands, Queensland and Mr Phil Hadlington, Forestry Commission of N.S.W., Sydney, other species of insects were imported into South Africa (Cilliers, 1977), the imported insects are listed in Table 2. Host specificity tests were done in Hawaii, Trinidad and Australia (Harley, 1969; Harley & Kunimoto, 1969; Harley & Kassulke, 1971; 1974). These tests were regarded as sufficient for our requirements, and permission was granted to release the insects in South Africa.

Table 2: Insects introduced into South Africa for the biological control of *Lantana camara*.

Species	Importation into South Africa				Releases in South Africa			Present status
	Native Land	Source	Year	Number	Year	Number	Area	
Octotoma scabripennis Guérin			1968	1050 Adults	1971	450 Adults	Buffelspoort	Not established
		Australia	1971	3000 Adults	1971	1100 Adults	Pretoria	Not established
(Coleoptera :			1974	4759 Adults	1974–1975	7139 Adults	Nelspruit	?
Hispidae)	Mexico	Dept. Lands	1975	4765 Adults	1974–1975	2385 Adults	Margate	Established
			1976	5600 Adults	1976	600 Adults	Pretoria	Not established
			1976	4467 Adults	1976	2000 Adults	Mt. Edgecombe	Uncertain
			1976	4300 Adults	1976	3000 Adults	Nelspruit	?
			1978	39304 Adults	1978–1981	27101 Adults	Tzaneen	Established
					1979	16046 Adults	Shakaskraal	?
					1979	3246 Adults	La Mercy	Established
					1979	100 Adults	Buffelspoort	Not established
					1981		Natal & N Tvl	Still being released
Uroplata girardi Pic.			1968	1050 Adults	1974–1975	6700 Adults	Nelspruit	?
		Australia	1971	7 Adults	1975	3374 Adults	Margate	Established
(Coleoptera:	Brazil		1971	4330 Adults	1976	600 Adults	Pretoria	Not established
Hispidae)	Paraguay	Dept. Lands	1975	6744 Adults	1976	2500 Adults	Mt. Edgecombe	Uncertain
	Argentina		1976	5800 Adults	1976	3000 Adults	Nelspruit	?
			1977	2280 Adults	1978–1979	21796 Adults	Tzaneen	?
					1979	7954 Adults	Shakaskraal	?
					1979	3104 Adults	La Mercy	Established
					1979	100 Adults	Buffelspoort	Not established
					1981		Natal & N Tvl	Still being released
Octotoma championi Baly.	Costa Rica	Australia	1978	110 Adults	1978	300 Adults	Tzaneen	?
(Coleoptera: Hispidae)		Dept. Lands						
Uroplata sp. near *biliniata*	Costa Rica	Australia	1978	60 Adults	1978	300 Adults	Tzaneen	?
Chapius (Coleoptera: Hispidae)		Dept. Lands						

Table 2 – Continued

Species	Importation into South Africa				Releases in South Africa			Present status
	Native land	Source	Year	Number	Year	Number	Area	
Plagiohammus spinipennis (Thoms)	Mexico	Australia	1970	377 Larvae	1973	16	Pretoria	Garden establishment
			1971	136 Larvae	1975	82	Burgers Hall	?
			1972	160 Larvae	1975	169	Sabie River Bungalow	?
				159 Larvae	1976	46	Buffelspoort	?
(Coleoptera: Cerambycidae)		Dept. Lands	1973	400 Larvae	1976	16	Mt. Edgecombe	?
					1979	6	Margate	Not established
						32	Tzaneen	?
Teleonemia elata Drake (Hemiptera: Tingidae)	Brazil	Australia	1972	896 Adults	1972	104 Adults	Durban Bluff	Not established
	Chile	CSIRO				147 Adults	Piermaritzburg	Not established
Leptobyrsa decora	Peru	Australia	1972	490 Adults	1978–Feb.1981	23717 A&N*	Tzaneen	Uncertain
(Hemiptera: Tingidae)	Colombia	CSIRO	1973	1746 Adults	1978–1979	1300 A&N	La Mercy	Still being released
			1975	8000 A&N	1978–1979		La Mercy	
			1977	5000 A&N	1978–1980	6490 A&N	Buffelspoort	
			1980	5729 A&N	1978–1979	2000 A&N	Shakaskraal	
					1980	750 A&N	Margate	
					1981	1000 A&N	Pretoria	
Neogalea esula (Druce) (Lepidoptera: Noctuidae)	Southern California	Australia Dept. Lands	1968	156 Pupae	1968	60 Larvae	Pretoria	Not established
Autoplusia illustrata (Lepidoptera: Noctuidae)	Colombia	Australia Dept. Lands	1978	302 eggs				Not released cultures died in quarantine
Phytobia lantanae Frick. (Diptera: Agromyzidae)	Trinidad		1978	256 pupae				Not released cultures died in quarantine
		Australia	1980	600 pupae				
		CSIRO	1981	1000 pupae				

* A&N : Adults and Nymphs

As is shown in this study, the most effective of the insects, O. scabripennis and U. girardi, built up rapidly at Margate on the Natal South Coast and with T. scrupulosa repeatedly defoliated L. camara at the release site. These beetles are still being introduced into new areas in South Africa.

L. camara as a noxious, aggressive weed will probably need a complex of organisms to overcome its exceptionally vigorous growth. The insects already imported and/or available attack leaves, growth tips, flowers and seeds, and also girdle the stem. In the study presented here the combined effect of T. scrupulosa, O. scabripennis and U. girardi is evaluated. By means of destructive sampling the population trends of the insects, the increase in damage to leaves and flowers and the effects on the seed production were followed. In order to follow the growth pattern of L. camara, regular measurements were made of the branch diameter, internodal length, leaf size, lifespan of leaves, flower and seed production, the number of insects and the amount of damage by the insects on marked branches. These insect damage studies were done in an insecticidal exclusion trial at Margate and in pre-release studies at 4 other localities. At one such locality at Tzaneen, insect damage was determined in a large walk-in cage.

3. MATERIALS AND METHODS

Study areas

As there are so many L. camara forms or cultivars in the country, study areas were chosen where different lantana forms were dominant and in different habitats and climatic areas.

The two main sites chosen (Fig. 2) were Margate, on the Natal South Coast, where a pink lantana is dominant, and Letaba Estates, Tzaneen, northern Transvaal Lowveld, where a pink aggressive form dominates. Supplementary observations were made at 3 other sites: Buffelspoort, in the western Transvaal, Shakaskraal and La Mercy on the Natal North Coast. At Buffelspoort and La Mercy, pink cultivars are dominant, and at Shakaskraal an orange one. Other study areas (Fig. 2) with pink cultivars at Nelspruit and Burgers Hall in the eastern Transvaal Lowveld were destroyed by slashing, bulldozers or fire early in the programme, and these sites were abandoned. At all these sites pre-release studies were done first and were followed by studies to ascertain population build-up of the released insects and their impact on lantana.

Sampling the plant for insect damage

Destructive sampling was mainly aimed at revealing the population build-up of the insects and ascertaining leaf injury. One of the study insects, T. scrupulosa, completes its life cycle in 3 to 4 weeks, and the two hispids in 4 to 8 weeks. By taking monthly samples, the life cycle, population build-up and effect of these insects on the plants could be determined. The active stages of the insects mainly occur on the 10 terminal leaves. The later instars, especially of the hispids, feed on and defoliate the older leaves. Eventually, after considerable experimentation with sampling units of different sizes, it was decided that 50-cm lengths of branches, including the 10 terminal leaves and all secondary branches (side shoots), would be a reliable sampling unit for assessing insect populations and damage to leaves. A LSTATS program, P/Numobs, was then used to determine the optimal sample size. A sample of 17 or more branches (each 50 cm long) was found to give reliable results. In this study the sample size was fixed at 25 branches. Larger sample sizes did not significantly increase accuracy or significantly reduce the standard error of the sample mean.

Each 50-cm length of branch was divided into (i) the main branch and (ii) the side shoots; the following observations were made separately for (i) and (ii), and eventually related to insect damage.

- Number of leaves
- Leaf breadth
- Number of flowers
- Number of seed-heads (and number of berries on seed-heads)

In addition the following kinds of evidence of insect activity were recorded for hispids:

- Number of eggs per leaf
- Number of mines per leaf
- Number of adult hispids
- Number of leaves with feeding scars

and for the tingid:

- Number of leaves with egg batches
- Number of nymphs
- Number of adults
- Number of leaves with feeding scars

Appendix 1 is an example of a data sheet.

Leaf breadth and leaf area

The clearest manifestation of plant growth, and a factor that may vary in a very marked manner as a result of insect damage, is leaf area; but because it was difficult to measure leaf area in the field an indirect method was developed. A sample of 100 leaves was taken from each study area and the leaf outlines were traced on graph paper. The length and breadth were measured in millimeters, and the leaf area was determined by counting squares on the graph paper. A positive correlation was found between length and area and also between breadth and area. Subsequently, breadth was used as an estimate of area, as it was easier to measure in the field. The relationship between breadth and area was determined by a LSTATS P/Repol Program (revised IBM Scientific Subroutine Package) and described by a second degree polynomial $y = a + bx + cx^2$, where y = area (mm^2), x = breadth (mm), and a, b, c are constants (see appendices 2 & 3). This relationship holds good for all leaves, from all cultivars, that are more than 10 mm wide. Appendices 2 & 3 are the tables used, at two of the sites, for determining leaf area.

Insect exclusion experiments

The destructive sampling of the plant, to determine insect damage and population growth, could not be used to determine the impact of the insects on the growth of the plant, and an insecticidal exclusion trial was used to measure this. At Margate in 1978-79, where hispid and T. scrupulosa populations were high, ten lantana bushes were chosen. Five bushes received 40 g of 15% aldicarb at monthly intervals from October to May. The other five bushes were regarded as controls, and insects were allowed to build up on them. On each of these bushes four branches were marked in October, when the plants had already started growing actively, and the growth pattern was followed until May, then the plants become dormant with the onset of cooler weather. At Letaba, insect populations were allowed to build up in an outdoor cage (8 x 30 x 5 m). Branches were marked in the cage, and the branches outside the cage served as controls, as no insect build-up occurred in the field at Letaba.

The same parameters of insect damage and plant growth were measured as before, and in addition the stem diameter and the internodal length of both main branches and side shoots were recorded.

In following the plant growth pattern the exact number of leaves per branch and those abscised (lost or dead) could be determined. From such data it became evident that there was a difference between the longevity (leaf lifespan) of leaves damaged by the insects and of those that were not damaged. Longevity of leaves was therefore determined by measuring the average time a leaf remained on a branch under varying conditions, with and without insect attack. The formula

$$B = (L_n - L_i) + (D_n - D_i)$$

was used to calculate the number of leaves recruited into the leaf population on each sampling occasion; where B = the number of new-grown leaves; L_n and L_i = number of live leaves at time n and at an earlier time i; D_n and D_i = the total number of lost leaves (detected from the number of leaf scars i.e. scars left on the stem following leaf abscission) at times n and i. A polynomial regression (LSTATS P/Polreg by P.H. Kloppers) was then derived from these data and used to generate smooth curves for the number of leaves recruited and lost over a period of time. These curves were then used to determine the average longevity of leaves. In addition the percentage leaf area damaged by each species of insect or leaves lost was determined visually for 100 leaf sites and rated as follows.

	% Damage Rating
No damage	
<1%	
1% - 10%	
11% - 25%	
26% - 50%	
51% - 75%	
76% - 100%	
Defoliation (leaves lost).	

Appendix 4 is an example of the data sheet used for percentage damage rating.

4. BIOLOGY OF THE IMPORTED INSECTS

The biology of the four imported species is summarized in the following pages.

Ophiomyia lantanae

A brief account is given here of observations on the damage done by the seedfly, Ophiomyia lantanae, (Fig. 3) as the evaluation methods differ from those used for evaluation of the leaf-damaging species.

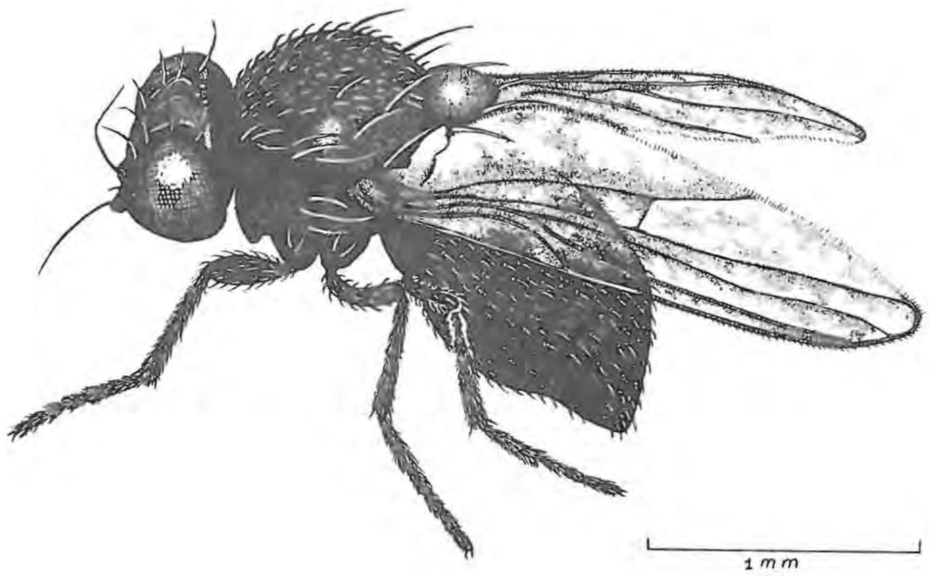

Fig. 3. The seedfly, Ophiomyia lantanae (Frogg.) (Diptera: Agromyzidae).

The seedfly oviposits in green berries and the maggots feed on the flesh of the berries. Pupation usually occurs in the ripe berries in a cavity between the two seed embryos or in the berry flesh, occasionally in the berry peduncle. The seed embryos are enclosed in the testa, and the larvae of O. lantanae were seldom found directly damaging the embryos. A generation is completed in about 21 days (Kachelhoffer et al., 1981), and it is estimated that there are 14 - 16 generations a year in South Africa. Populations reach peaks in early summer and autumn. Although the fly can breed throughout the year, it may overwinter as pupae. Females puncture the flower corolla and then feed at the puncture. Whether this feeding causes flowers to die is not known.

O. lantanae is generally regarded as of little value for the biological control of L. camara (Perkins & Swezey, 1924; Haseler, 1966; Greathead, 1971). In Hawaii the infestation of berries ranged from 70 to 86% (Perkins & Swezey, 1924). Haseler (1966) mentioned that up to 75% infestation of berries is common in Australia. In South Africa infestations range from 4 to 100%. In Pretoria dissections of green and ripe berries from a pink L. camara were made for two years (1977 - 1979). Fifty green and fifty ripe berries were collected at random every week and dissected to ascertain the condition of the two seed embryos and whether seedfly infestation was present. Embryos were recorded as either fully developed (mature) or shrunken. Only larvae, pupae, feeding damage and exit holes were regarded as indicating seedfly infestation. Of 2700 green berries dissected, 30% were infested by the seedfly, and of 3250 ripe berries dissected, 55% were infested. Table 3 gives the percentage of mature and immature embryos found in infested and uninfested green and ripe berries.

Table 3: Number (and percentage) of mature (ME) and shrunken (SH) embryos in infested and uninfested green and ripe berries

	Green berries (2700 dissected)			Ripe berries (3250 dissected)		
	ME	SH	TOTAL	ME	SH	TOTAL
Infested	498	1094	1592	698	3021	3719
Uninfested	2292	1516	3808	1151	1630	2781
Total seed embryos inspected (2 per berry)			5400			6500

Fewer green berries than ripe ones were infested by the fly, although the fly oviposits in green berries. Eggs were not counted as infestations in these dissections, but Kachelhoffer et al., (1981) showed that more green berries were infested when eggs are taken into account. In Table 3 the difference between the numbers of shrunken embryos in infested and uninfested green berries is highly significant, and the same applies to ripe berries ($P << 0,001$ in both cases using 2 X 2 contingency tables and Chi square). The presence and feeding of the fly maggot thus increases the number of shrunken embryos. But the key to assessing the true effect of infestation lies in germinating the infested and uninfested berries to find whether there is any difference. All attempts to germinate them failed, and this problem has been handed over to a plant physiologist.

The only reference to the influence of the fly on embryo development is by Perkins & Swezey (1924), who recorded that in one batch of infested berries, 75% of the embryos were shrunken, while in two other batches they recorded 83 - 89% shrunken embryos. They found that both infested and uninfested berries were slow to germinate and that the difference in the number of seedlings produced was not great enough to be of practical importance.

In South Africa O. lantanae is attacked by parasitoids in five families; Braconidae, Cynipidae (subfamily Eucoilinae), Eulophidae (Euderus sp.) and Eupelmidae. The braconids were very common. Unfortunately none of the parasitoids can as yet be identified to species level.

O. lantanae is not further dealt with in this study.

Teleonemia scrupulosa

The life history of T. scrupulosa has been studied in Fiji, India and Australia (Simmonds, 1929; Fyfe, 1937; Khan, 1945; Roonwal, 1952; Harley & Kassulke, 1971) and by me in South Africa.

The eggs, in batches of 4 - 40, are inserted into the main veins or midrib of the underside of young leaves at the end of young actively growing shoots. Eggs are sometimes also laid in young stems, petioles or flower stalks. The operculum of the egg protrudes from the plant tissue. The egg group has the appearance of an irregular row of tiny dark-whitish to brown dots on the leaf. Where eggs are present on the underside of leaves, the adjacent plant cells die and growth ceases, but growth continues on the upperside, with the result that the leaves tend to curl downward and become stunted. At summer temperatures of 24 - 29°C, eggs hatch in 6 - 8 days, the incubation period increasing as temperatures drop. Between 14° and 21°C, eggs hatch in 11 - 22 days, below 16°C eggs may overwinter, and below 14°C they may not hatch. As all eggs in a batch are not laid at the same time, hatching extends over several days..

The nymphs are dull brown and have prominent spines along the margin and mid-dorsum of the abdomen. They feed in groups on the underside of leaves between the veins, where moulting also occurs. The feeding area is dotted by black drops of excreta. There are five distinct instars. Wing buds are visible in the fourth instar and well developed in the fifth instar. Each of the first four instars are of about 3 days duration and the fifth instar takes about 5 days or more at summer temperatures. The nymphal stages last 12 - 15 days at 24 - 29 °C and 15 - 18 days at 21 - 25°C. At still lower temperatures of 17 - 13°C, the nymphal duration rises to 20 - 33 days, and mortality is high below 14°C. The nymphs of the first four instars are sluggish, but those of the fifth are more mobile and tend to migrate to adjacent leaves, flowers or buds. Migration is forced upon them when a leaf dries out, drops, or becomes overcrowded.

Newly moulted adults are at first white with red eyes, but within two to three hours they become pale brown. The adult (Fig.4) is small (average length 3,5mm) and elongate, with the pronotum extending beyond the bases of the forewings; the latter are pitted, with prominent longitudinal ridges. The forewings and pronotum are finely pubescent. The forewings are slightly constricted about two-thirds down their length, widening again

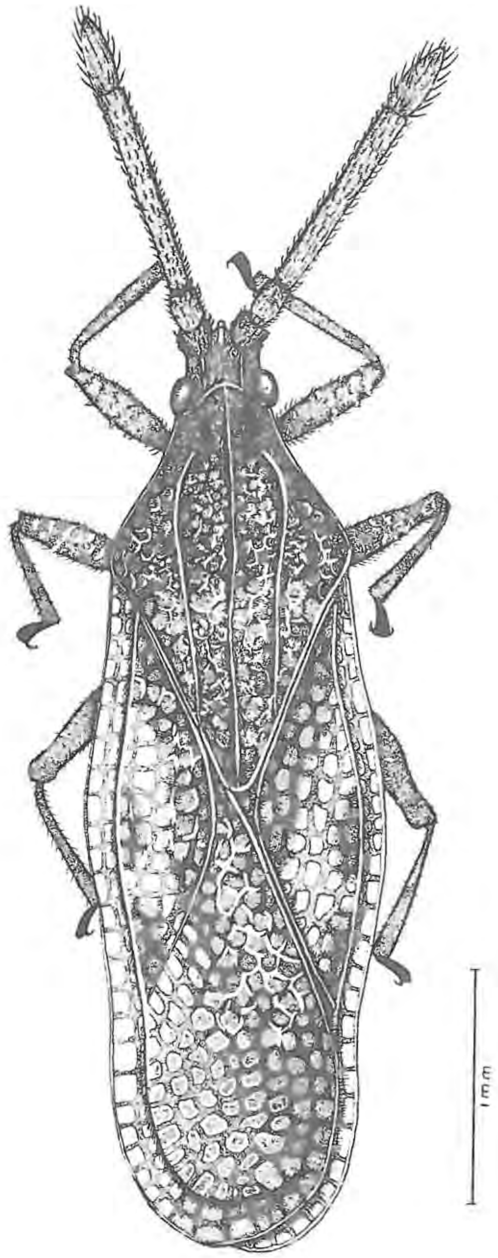

Fig. 4. Teleonemia scrupulosa.

towards the distal edges. The wings also bear large hyaline areoles. The pilose antennae have four segments, of which the third is the longest (Drake, 1918; Roonwal, 1952). Mating occurs within the first four days and oviposition commences after 5 - 7 days. T. scrupulosa females are moderately fecund - 89 eggs have been recorded per female - and the relatively short life cycle of three to four weeks allows for rapid build-up of populations. Adults feeding on flowers and leaves are more fecund than those feeding on leaves only (Radunz, 1971). In winter the adults live for up to five months, in summer up to three months, with egg-laying stretching over seven weeks. The sex ratio is about 1,3:1 (males to females) in insectary-reared material, and 1:1 in field-collected material (Khan, 1945). I recorded a sex ratio of about 1,5:1 among 76 individuals in field-collected South African material. Generations tend to overlap, and it is not uncommon to find three generations together. It is estimated that there are between 9 and 11 generations a year in South Africa. Mortality is very high in winter and during periods of heavy rain (Khan, 1945). Populations reach a peak in midsummer, generally after about three generations. T. scrupulosa exhibits a marked preference for certain lantana varieties (Radunz, 1971), but causes similar damage to all varieties.

T. scrupulosa has piercing and sucking mouth parts. When a cell is punctured the entire contents are sucked up, and this results in leaf chlorosis. At first the adults and nymphs feed mainly on the underside of leaves, but migrate to flowers and buds, and on warm days the adults fly and disperse. The feeding marks show as white specks on the upper side of a leaf. Very young leaves become distorted and do not extend fully. Leaves dry up from the tip and sides and in time also turn silver and brown before drying up and dropping. Feeding on the tubular part of the flowers causes them to shrivel, turn brown and die; buds that are fed on also turn brown and become sticky. When plants are defoliated, feeding also occurs on young stems (Fyfe, 1937; Harley & Kassulke, 1971). The feeding of T. scrupulosa apparently has systemic effects on plant growth, as young terminal growth showing no signs of having been attacked becomes distorted and dies (Fyfe, 1937; Harley & Kassulke, 1971). The die-back of internodes and whole branches may also be due to the absence of leaves or to the mechanical killing of plant cells caused by feeding and blockage of the plant transport system.

The effect of T. scrupulosa infestation on the plant is delayed, and defoliation occurs only after a time, when the population has built up and reached a peak in midsummer.

The natural enemies of T. scrupulosa in South Africa are few. Apart from spiders, which are non-specific predators, larval mites of the genus Bochartia sp. (Erythraeidae) attack T. scrupulosa in the coastal areas. The incidence of these mites on the tingid is very low. Bochartia sp. is a general predator of insects (Dr M.K.P. Meyer, personal communication). Simmonds (1929) found a predatory bug, Germalus pacificus Kirk (Lygaeidae), to be important in Fiji, and Fyfe (1937) recorded spiders, coccinellids and neuropteran larvae preying on T. scrupulosa, and also recorded a parasitic fungus, Hirsutella sp. In Australia, Nabis capsiformis Germ. (Reduviidae) was recorded as a predator (Fyfe, 1937).

Octotoma scabripennis and Uroplata girardi

Apart from the work of Harley (1969), very little has been published on the life cycles of these two beetles. O. scabripennis is native to Mexico and U. girardi comes from Brazil (Krauss, 1962) (Table 2). Their life cycles are very similar.

The egg of both species is nearly hemispherical and is inserted into the upper surface of the leaves and covered with black material, which resembles excreta but which is possibly from the collaterial glands (Harley, 1969). Eggs are always laid singly and often next to a feeding scar (Fig.5). The incubation period for the eggs of both species is 10 - 14 days. On hatching, the larva immediately tunnels into the leaf, feeding on the mesophyll and leaving both the upper and lower epidermis intact. A more or less central area is enlarged and becomes tightly packed with black excreta on the walls. From this central area tunnels extend in various directions. There are three larval instars (Fig. 6).

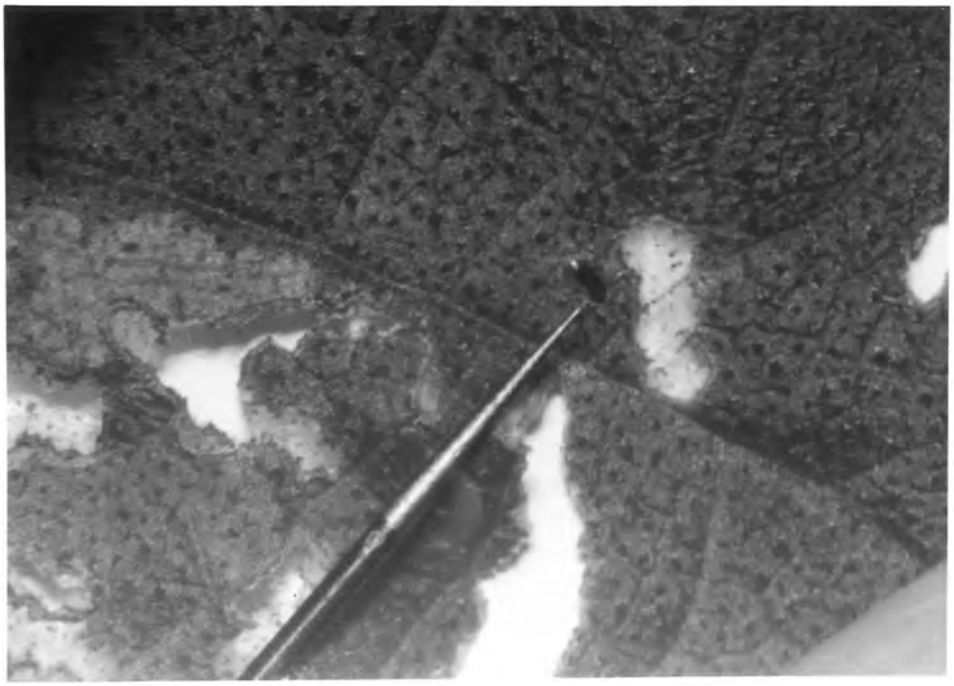

Fig. 5. Hispid egg next to feeding scar of adult.

Fig 6. Larvae and pupa of Octotoma scabripennis. Those of U. girardi are very similar.

The mean breadth in mm, with the range in brackets, of the head capsules of the three larval instars of U. girardi are (i) 0,37 (0,30 - 0,38). (ii) 0,52 (0,50 - 0,54). (iii) 0,76 (0,70 - 0,82). The corresponding measurements for O. scabripennis are (i) 0,42 (0,40 - 0,48). (ii) 0,59 (0,56 - 0,62). (iii) 0,86 (0,84 - 0,90). O. scabripennis larvae are thus usually bigger than those of U. girardi. Larvae of both species are yellow with brown heads. The larval stages are completed in 12 - 20 days. Larval mortality increases in autumn, and very few larvae are present throughout winter. The entire larval life is spent in one blotch mine on the same leaf. If a leaf drops before the last larval stage is well advanced the larva dies.

The pupal stage lasts 8 - 14 days. Pupae are also yellow and are always found in the central dark enlarged area of a mine.

Fig. 7. O.scabripennis adult just before leaving a mine in a leaf of Lantana camara.

The adult remains in the mine (Fig. 7) for a day or two before moving to the leaf surface. The life cycle from egg to adult takes

30 - 40 days. Harley (1969) states that U. girardi develops from egg to adult in 37 - 40 days and O. scabripennis in 34 - 45 days in Australia.

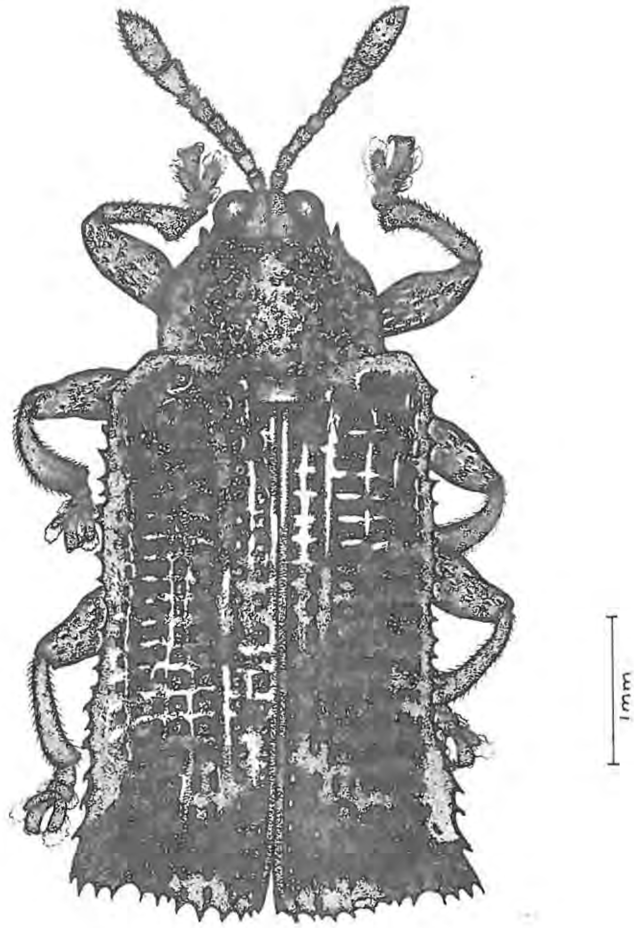

Fig. 8. Uroplata girardi.

U. girardi adults, (Fig.8) are on average 4,6 mm long and are reddish brown with the elytra and thorax darker than the legs and abdomen. On the lower half of the elytra are eight lighter-coloured areas. The elytra are deeply pitted, the pits being arranged in longitudinal rows with ridges between the rows. The outer and hind edges are serrated. The thorax is also deeply pitted like the elytra and legs. The antennae are eight-segmented.

Fig. 9. Octotoma scabripennis.

Adults of O. scabripennis are black with a brownish tinge to the thorax and average 5,8 mm in length. The elytra are elaborately patterned with irregular ridges and longitudinal rows of pits (Fig. 9). The outer and hind edges of the elytra are serrated. The pitted thorax is reddish-brown with four dark areas. The legs are reddish-brown with lighter areas at the joints. The antennae are of the same colour as the legs and are eight-segmented.

Adults of both species feed on the upper surface of leaves, leaving the lower epidermis intact. Feeding scars are elongated and irregularly shaped (Fig.10). U. girardi scarifies leaf edges and this area then curls up and is used as a shelter, which is also used by O. scabripennis (Fig. 11).

Fig. 10. Old hispid mines and adult feeding scars in leaves of Lantana camara.

Fig. 11. Curl of leaf edges due to adult Uroplata girardi feeding.

In the pre-oviposition period of 3 to 4 weeks the adults feed extensively (Harley, 1969). Although the lower epidermis is left intact when the beetles feed, it eventually collapses, and an irregular hole is then left in the leaf.

Both species exhibit facultative diapause. The onset of diapause coincides with a fall in temperature, a shortening day-length, and the onset of unthriftiness of the plant. The entire adult population of O. scabripennis goes into diapause from early winter to the middle of spring, but part of the U. girardi population remains active during this period in Australia (Harley, 1969). In South Africa very little activity, except occasional feeding by the adults, has been observed in winter. Both beetles have three generations per year.

U. girardi appears to prefer semi-shaded cooler conditions and O. scabripennis exposed hotter conditions (Krauss, 1962; Harley, 1969). In South Africa, the former species is dominant in the coastal area and the latter in the inland areas, at a higher altitude. The exact longevity of the adults is not known but field observations in South Africa suggest that it is about three to four weeks. Diapause lasts 12 weeks or more.

Fig. 12. Hispid mines in leaf of Lantana camara.

Feeding by adults and mining by larvae causes severe damage to leaves, especially where there is more than one mine in a leaf (Fig.12). The affected leaves usually remain attached to the plant until the emergence of adult beetles, after which they soon drop off. Damage is most marked in March to April, when populations have reached their peaks in the third generations.

Natural enemies of these insects, even where the beetles are indigenous, are few. Krauss (1964) reared Spilochalcis sp. (Chalcididae) and Calliephialtes sp. (Ichneumonidae) from larvae of O. scabripennis in Mexico. At Letaba in the northern Transvaal the parasitic mite Pyemotes ventricosus (Newport) was found on larvae of O. scabripennis.

Dicladocerus sp. (Eulophidae) has been reared from the larvae of U. girardi (Krauss, 1964), but has not been recorded in South Africa. On one occasion at Margate a pupa of an unidentified eulophid was found in a larval mine of U. girardi. In Trinidad a predatory vespid was recorded on the larvae of U. girardi (Harley, 1969).

5. RESULTS OF DESTRUCTIVE SAMPLING

Insect population fluctuations

Teleonemia (T. scrupulosa) had already been firmly established at the Margate site chosen to release the two beetles. Octotoma (O. scabripennis) and Uroplata (U. girardi). The beetles were released there in November/December 1974 - February 1975 (Table 2). Although fire destroyed the plants on part of the site in the winter of 1975, populations of the beetles increased steadily, and by February 1976, there was an average of 9% of leaves with mines, which rose to 26% by December, 1976. In February 1977 some of the plants were destroyed by slashing, but on those that remained it was evident that damage by Teleonemia and the beetles had increased to the point where plants were beginning to lose leaves excessively. In April and June, leaf loss averaged 21% and 32%. In July 1977 the site was again ravaged by fire, but regrowth in September was such that sampling could be started. At each sampling date, for the next three seasons, 25 branches, each 50 cm long, were cut and counts (see Materials and Methods) were done immediately. A "season" lasted from August until May or June each year. In August the host plants are still dormant, showing very little growth, and the insects are mostly still inactive. With the onset of the first spring showers and warmer weather, growth of the host plants resumes and the insects become more active. The rest of the season is a period of conflict between the depredations of the insects and the recuperative powers of the plants, which it is the purpose of this thesis to describe.

The part of the lantana plant that all three insects chiefly damage is the leaves. In the next two sections an account is given of fluctuations in the populations of the insects and in the amount of damage they did to leaves during three successive seasons from 1977 to 1980.

The data from this Margate experiment are given in Tables 4 & 5 from which the graphs (Figs 13 & 14) have been drawn showing the insect population fluctuations. Included in both figures are rainfall and temperature records for the relevant period, recorded at Port Shepstone, the closest Weather Station to Margate (Daily Weather Bulletin, Weather Bureau, Department of Transport, Republic of South Africa, October 1977 to May 1980). The results for main branches and side shoots were recorded separately, but are combined in Tables 4 & 5 and in Figs 13 & 14.

Table 4: *Lantana camara:* Number of leaves on samples of 25 branches on which hispids and *Teleonemia* were recorded. Destructive sampling, Margate, 1977–80.

Date	Total number of live leaves	Hispids: Number of leaves with eggs	Total number of eggs	Number of leaves with larvae	Total number of live larvae (older instars in brackets)	Number of leaves with dead larvae	Total number of dead larvae	*U. girardi* adults	*O. scabripennis* adults	Total adults	*T. scrupulosa*: Eggs*	Nymphs	Adults
77.09.28	1610	87	201	0	0 (0)	0	0	22	0	22	0	12	0
77.11.02	1247	60	73	153	170 (186)	1	2	1	1	2	528	3	2
77.12.12	1266	18	32	76	30 (75)	0	0	38	0	38	1518	233	29
78.01.12	1236	88	195	35	43 (12)	2	3	34	6	40	2332	257	142
78.02.14	752	53	86	134	139 (6)	10	14	3	2	5	462	4	30
78.03.18	676	81	152	83	100 (3)	11	11	29	2	31	418	9	6
78.04.27	1134	234	482	164	225 (78)	25	47	25	5	30	110	0	0
78.06.16	1067	34	60	91	25 (87)	48	75	24	0	24	132	0	0
78.08.22	901	10	32	3	10 (1)	7	17	45	4	49	88	3	3
78.09.26	793	31	60	0	0 (0)	0	0	76	4	80	242	57	4
78.10.25	896	169	308	52	1 (90)	0	0	19	4	23	132	0	1
78.11.23	975	43	64	131	137 (70)	13	25	0	0	0	44	64	8
78.12.19	865	3	4	49	12 (39)	14	15	9	0	9	418	5	8
79.01.17	871	24	36	33	31 (18)	8	10	25	7	32	2508	1020	74
79.02.15	786	61	75	81	98 (11)	7	12	9	0	9	1034	0	10
79.03.15	1029	26	32	78	220 (22)	1	3	3	1	4	1606	12	6
79.04.10	1188	24	34	60	61 (19)	44	58	7	1	8	506	0	0
79.05.08	1059	14	34	22	21 (10)	14	14	11	2	13	418	0	0
79.08.15	868	0	0	0	0 (0)	3	3	12	0	12	286	0	0
79.09.11	1176	3	7	1	1 (0)	0	0	14	1	15	110	27	0
79.10.16	936	66	129	57	116 (0)	1	1	2	0	2	880	44	23
79.11.21	948	7	9	99	59 (64)	9	15	1	0	1	836	76	8
79.12.18	966	0	0	57	13 (52)	4	4	26	0	26	2486	348	62
80.01.21	943	82	157	107	207 (2)	3	3	14	0	14	3300	197	84
80.02.19	727	55	108	56	75 (4)	14	18	6	0	6	1474	172	23
80.03.18	1219	50	67	62	73 (7)	8	18	11	0	11	814	3	3
80.04.21	1008	13	15	47	66 (8)	15	44	7	0	7	110	0	0
80.05.21	1226	10	16	25	33 (1)	48	63	22	0	22	66	1	2

* Numbers derived from Table 5.

Table 5: *Lantana camara:* Number of leaves showing hispid and *Teleonemia* damage, on samples of 25 branches. Destructive sampling, Margate, 1977–80.

Date	Total live leaves	Total leaf area (cm^2)	Lost leaves	*Hispids*				*T. scrupulosa*			Total leaves damaged
				Leaves with live larvae in mines	Leaves with dead larvae & vacated mines	Leaves with feeding scars	Total damage	Leaves with eggs	Leaves with feeding scars	Total damage	
Sept.	1610	21378	0	0	–	–	0	0	0	0	0
Nov.	1247	17565	23	356	2	–	358	24	1	25	383
Dec.	1266	20726	66	105	32	–	137	69	35	104	241
Jan.	1236	19433	155	55	29	36	120	106	146	252	372
Feb.	752	10091	680	145	25	44	214	21	3	24	238
Mar.	676	15238	926	103	60	55	218	19	59	78	296
Apr.	1134	18530	44	303	84	477	864	5	0	5	869
June	1067	16867	47	112	137	92	341	6	0	6	347
Aug.	901	12030	90	11	103	53	167	4	0	4	171
Sept.	793	10715	96	0	58	98	156	11	4	15	171
Oct.	896	12025	227	91	12	236	339	6	3	9	348
Nov.	975	13394	268	207	32	28	267	2	43	45	312
Dec.	865	13453	449	51	31	9	91	19	7	26	117
Jan.	871	14405	529	49	103	53	205	114	147	261	466
Feb.	786	10694	772	109	51	62	222	47	78	125	347
Mar.	1029	10045	965	242	13	35	290	73	47	120	410
Apr.	1188	10205	1221	30	137	73	290	23	9	32	322
May	1059	11525	921	31	62	57	150	19	8	27	177
Aug.	868	7287	1397	0	16	32	48	13	3	16	64
Sept.	1176	10547	925	1	9	36	46	5	7	12	58
Oct.	936	12036	337	116	3	55	174	40	24	64	238
Nov.	948	10909	722	123	35	31	189	38	36	74	263
Dec.	966	11282	701	65	79	42	186	113	168	281	467
Jan.	943	9861	2128	209	18	148	375	150	391	541	916
Feb.	727	8656	3158	79	35	190	304	67	258	325	629
Mar.	1219	13246	2574	80	18	146	244	37	153	190	434
Apr.	1008	10193	1959	74	93	201	468	5	27	32	500
May	1226	13156	1866	34	87	195	316	3	78	81	397

– Not recorded

* The numbers of leaves with eggs are recorded. On average, each egg batch contains 22 eggs so that the number of eggs recorded for *T. scrupulosa* in Table 4 is the product of the leaf number multiplied by 22.

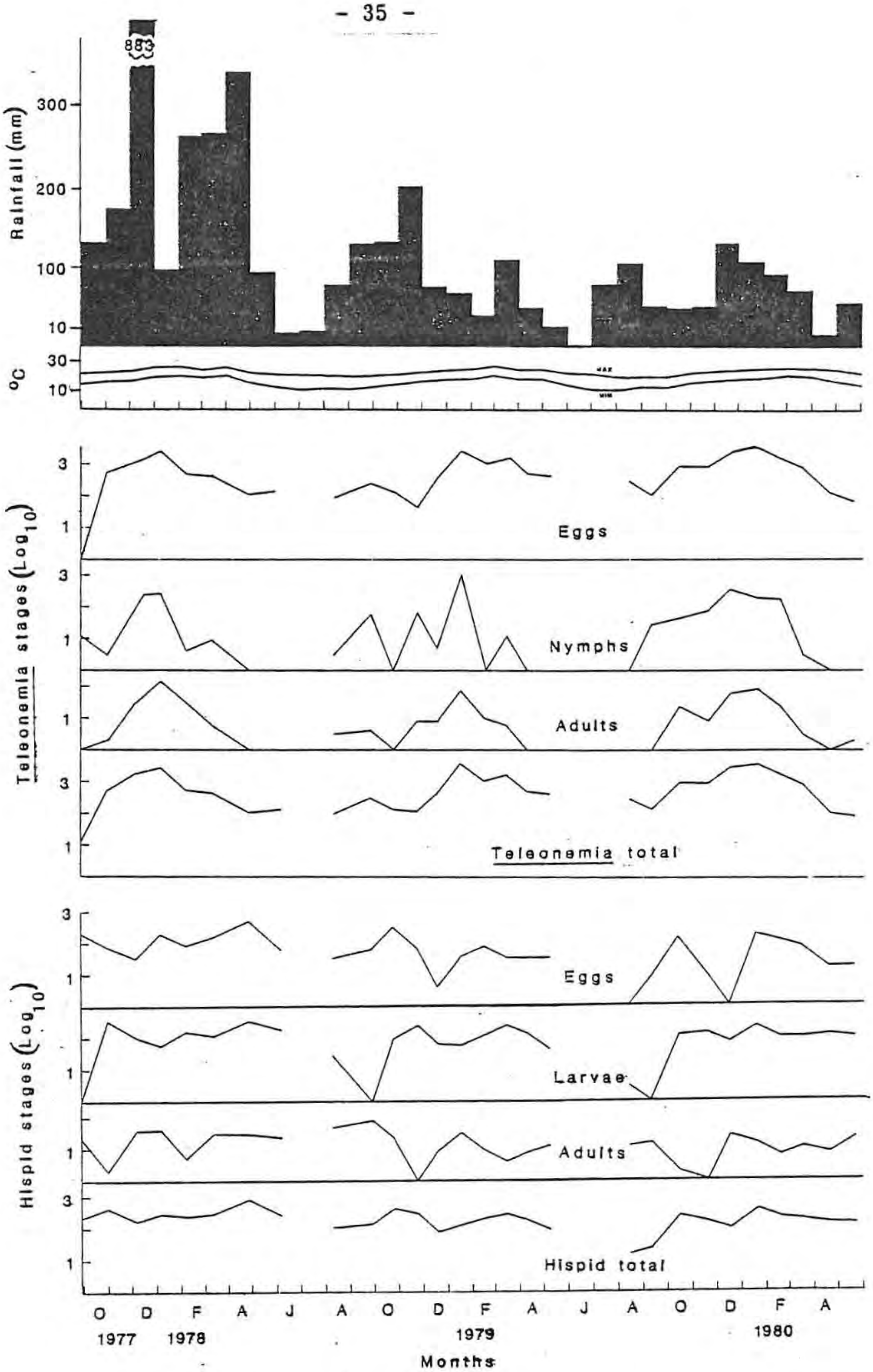

Fig. 13: Population fluctuations of the hispids and Teleonemia. Destructive sampling, Margate, 1977-80. Monthly rainfall (mm), monthly mean and maximum temperatures, at Port Shepstone, 1977-1980.

Hispid populations: Overwintering adults of the hispids started laying eggs in August-September. Larvae of the first generation reached high numbers in October-December and the first generation itself was completed by December-January (Fig. 13). The second and third generations overlapped. In Fig. 13 all stages of hispids were present from October-May every year. The adults of the third generation entered diapause after laying some eggs. Egg mortality was high, 26% in June 1977, indicating that low temperatures are detrimental, since less that 10% egg mortality was usually recorded in the summer months. The numbers of dead larvae rose towards the end of every season. There were peaks of adult numbers in August-October, December-January and again in March-May. Adults of Uroplata outnumbered those of Octotoma by 11:1 in 1977-78, 8,9:1 in 1978-79 and 115:1 in 1979-80; thus Uroplata was always dominant.

Teleonemia populations built up rapidly each season to a peak in about December-March consisting mainly of third-generation individuals. The rapid decline in numbers from March to May was due to dispersal and was associated with lower temperatures (Fig. 13). Teleonemia mortality could not be calculated in the field, as eggs need to be examined under a microscope to determine whether they are viable and adults and nymphs drop off the plant when dead.

Amount of insect damage to leaves

The data on leaf damage given in Table 5, are summarized in Fig. 14. As can be seen in Fig. 14 hispid damage exceeded that of Teleonemia except in 1979-80 which was drier than the other two seasons in this coastal area (Fig. 14). Fig. 14 indicates that the total number of leaves damaged was not significantly different from year to year, but this is misleading because the numbers of leaves lost due to insect damage is not recorded in the figure. How many leaves were lost through insect damage and how many through natural abscission could not be determined but since the numbers lost were probably similar from season to season the conclusions are not affected. Also, it is known that the damage

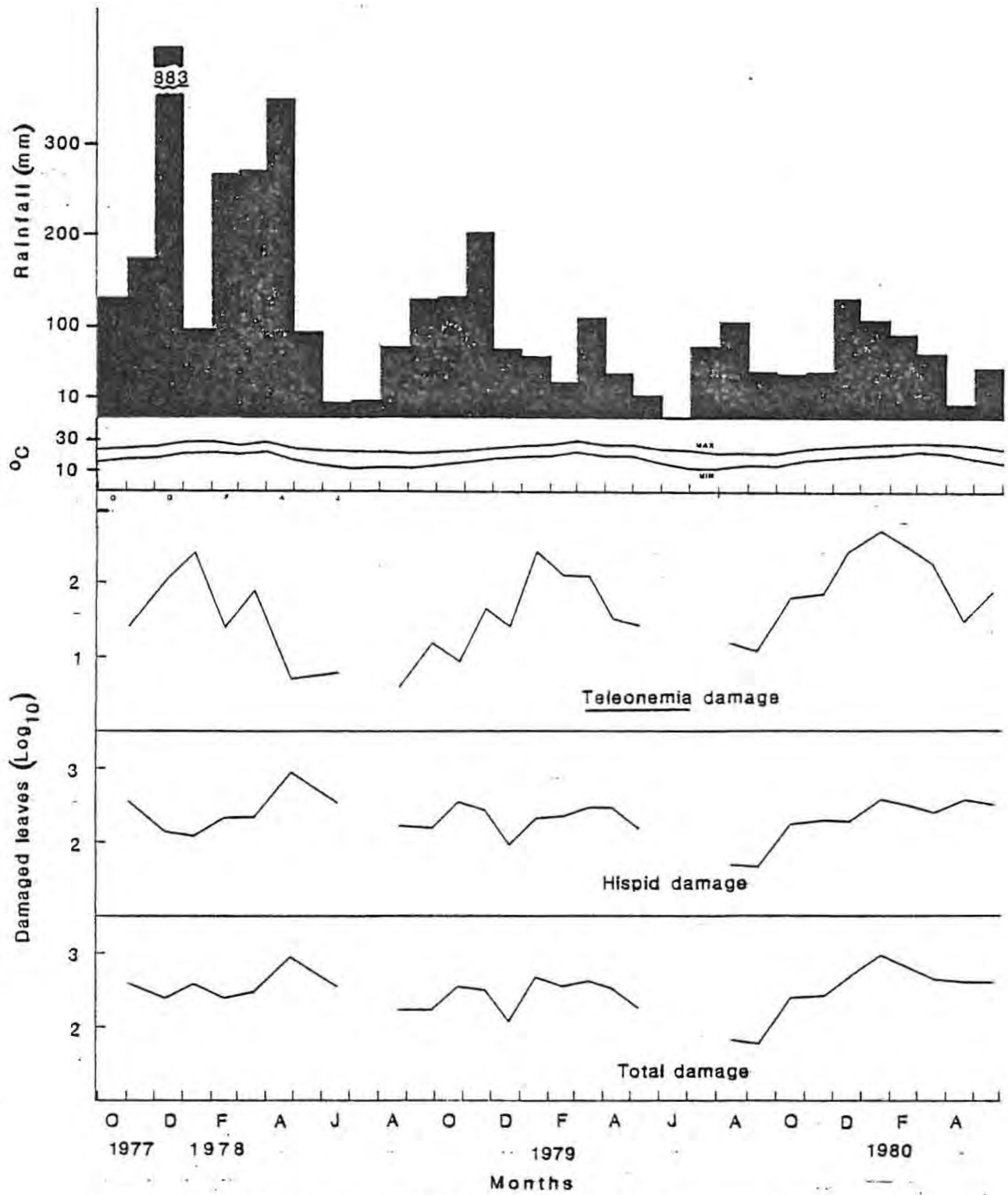

Fig. 14: Lantana camara: Leaves showing hispid and Teleonemia damage. Destructive sampling, Margate, 1977-80. Monthly rainfall (mm), monthly mean and maximum temperatures at Port Shepstone, 1977-80.

ultimately caused by all three insects is excessive leaf loss to the point of total defoliation.

The peaks of lost leaves in February-March (Table 5; Fig. 15) coincided with peaks in insect populations (Fig. 13). In 1977-78 the plants were defoliated in February-March, but recovery was complete by April. Thus, L. camara responds to severe defoliation by producing new leaves. The amount of insect damage to leaves remained high on the new and old leaves. Both hispid and Teleonemia damage levelled off as winter approached (Fig. 14) and insect populations declined (Fig. 13). The high incidence of lost leaves in February-March was associated with a slight decrease in the numbers of leaves damaged because most severely damaged leaves dropped.

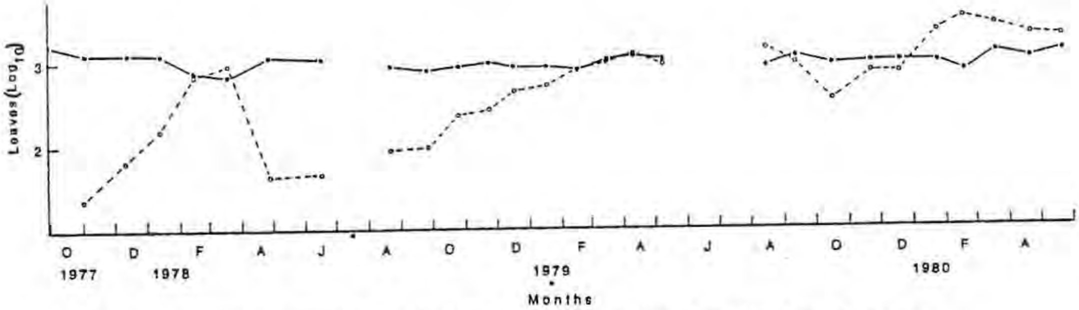

Fig.15: *Lantana camara*: Live leaves •—• and lost leaves o--o, due to attack by hispids and *Teleonemia*. Destructive sampling, Margate, 1977-80.

During July 1978 a fire passed through a small part of this site and counts were restarted in August. The plants were still dormant, with mature, hard and rather yellow leaves and very little new growth. The Teleonemia population was still low, but the hispids had already started to lay eggs (Fig. 13). Lost leaves on the main branches reached a peak in February-April 1979 and on the side shoots the main defoliating period was from January to May. The overall higher level of lost leaves can be attributed to the higher level of insect damaged leaves in October-November and again in April, while Teleonemia and hispids together caused another peak in lost leaves in January-February (Table 6 and Fig. 15).

In 1979-80 season was drier than the previous two seasons, and in August the numbers of Teleonemia adults and nymphs were low, as were those of the larvae and adults of the hispids (Fig. 13). Leaf damage was also lower than in the previous seasons, but numbers of lost leaves were higher (Figs 14 & 15). The increase in lost leaves recorded after the winter is due to the dry conditions and the natural shedding of old mature leaves that remained on the plant during winter.

The higher number of leaf sites (live leaves and lost leaves) per 50 cm branch in 1979-80 (Tables 5 & 6) may be due to the drier season but could be the effect of continued insect attack, which by reducing the vigour of the plant would results in shorter internodes and therefore more leaf sites per 50 cm branch. It was also evident that the lost leaves were very numerous in the 1979-80 season (Fig. 15). The insect populations recorded were not very high (Fig. 13), but the greater numbers of lost leaves indicate that the insects caused relatively more damage than in the previous seasons (Fig. 14).

It is clear from the results that populations of Teleonemia and hispids do not reach peaks at the same time, so that the insect stress on the plants is exerted throughout late summer (Figs 13 & 14). The hispids oviposit and mine in older leaves, whereas Teleonemia oviposits in and feeds on younger leaves.

Number of leaves and leaf area

From Table 6 it can be seen that on the main branches there was a marked decline in total leaf area in about January-March each season which coincided with a peak in the numbers of lost leaves and damaged leaves, and a decline in the number of live leaves. The bigger, i.e. the older, leaves tended to be abscised first. From March on there was an increase in leaf area because insect populations were low and because of the rapid expansion of young leaves. In April more new leaves were produced, with a consequent small increase in total leaf area. Leaf size, as indicated by mean leaf area, decreased on branches over the three seasons, leaves being smallest in 1979-80. This was probably due partly to the progressively lower rainfall and partly due to the effects of continued insect pressure over the three seasons. The leaf areas in Table 6 are not true measurements of total photosynthetic area as the areas per leaf that were removed by insect feeding were not calculated. The area damaged by egg laying of the hispids is always very small, but the area removed by larval mines and adult feeding may amount to more than 75%. The leaf curl and stunted growth that occurred where Teleonemia had laid eggs in the main veins, caused up to 50% reduction in leaf area. Feeding by the hispid adults and Teleonemia adults and nymphs caused leaves to dry out before they eventually abscised. Kachelhoffer et al. (1981) showed that leaves fed on by Teleonemia dropped sooner than undamaged leaves even when only 20% of the area was damaged.

The percentage damage (see Materials and Methods) recorded in the 1979-80 season give a better picture of the photosynthetic area removed by insects than the total areas given in Table 6.

Table 7 gives percentage damage to leaves and the different causes of damage to the leaves and the total number of leaves damaged per 100 leaves are shown diagrammatically in the histograms of Fig. 16. From Fig. 16 it is evident that leaf damage is greatest in (October-November) before defoliation and that most of the damage to leaves was done by the hispids. It is possible that leaves

Table 6: *Lantana camara:* Number of live leaves, total leaf area (cm^2), leaf area/100 live leaves, average number of leaves and mean leaf area on samples of 25 branches. Destructive sampling, Margate, 1977–80.

Date	Main branches					Side shoots				
	Live leaves	Total leaf area (cm^2)	Leaf area/ 100 live leaves (cm^2)	Mean number of leaves/ branch	Mean leaf area (cm^2)	Live leaves	Total leaf area (cm^2)	Leaf area per 100 leaves (cm^2)	Mean number of leaves/ branch	Mean leaf area (cm^2)
Sept.	518	13822	2668	21	26,7	1092	7556	692	7	6,9
Nov.	476	10773	2263	19	22,6	771	6792	881	5	8,8
Dec.	424	11068	2610	17	26,1	842	9658	1147	7	11,5
Jan.	440	9987	2270	18	22,7	796	9446	1187	8	11,9
Feb.	335	5721	1708	13	17,1	417	4370	1048	3	10,5
Mar.	395	8015	2029	16	20,3	281	7223	2570	2	25,7
Apr.	414	10289	2485	17	24,9	720	8241	1145	7	11,4
June	526	10981	2088	21	20,9	541	5886	1088	10	10,9
Aug.	510	8262	1620	20	16,2	391	3768	964	10	9,6
Sept.	607	9018	1486	24	14,9	186	1697	912	9	9,1
Oct.	582	9169	1575	23	15,8	314	2856	910	6	9,1
Nov.	429	8894	2073	17	20,7	546	4500	824	6	8,2
Dec.	410	8508	2075	16	20,8	455	4945	1087	13	10,9
Jan.	354	7852	2218	15	22,2	517	6553	1268	8	12,7
Feb.	275	5159	1876	11	18,8	511	5535	1083	7	10,8
Mar.	195	2252	1155	8	11,5	834	7793	934	9	9,3
Apr.	213	2315	1087	9	10,9	975	7890	809	7	8,1
May	298	4791	1608	12	16,1	761	6734	885	7	8,8
Aug.	267	2918	1093	11	10,9	601	4369	727	6	7,3
Sept.	337	4164	1236	14	12,3	839	6383	761	7	7,6
Oct.	526	7810	1485	21	14,8	410	4253	1037	8	10,4
Nov.	421	6114	1452	17	14,5	527	4795	910	8	9,1
Dec.	428	6714	1569	17	15,7	538	4568	849	7	8,5
Jan.	205	3088	1506	8	15,1	512	6773	1323	3	13,2
Feb.	133	1929	1450	5	14,5	594	6727	1132	3	11,3
Mar.	171	3043	1780	7	17,8	1048	10203	974	4	9,7
Apr.	240	3934	1639	10	16,4	768	6259	815	4	8,1
May	239	3838	1606	10	16,1	987	9318	944	5	9,4

Table 7: *Lantana camara:* Number of leaves undamaged, number lost, and ratings for percentage of leaf area damaged by hispids, *Teleonemia* and from other causes.

Date	Leaves with no damage	Leaves lost	Rating for Hispids						Rating for *Teleonemia*						Rating Other damage					
			<1	1–10	11–25	26–50	51–75	76–100	<1	1–10	11–25	26–50	51–75	76–100	<1	1–10	11–25	26–50	51–75	76–100
						%						%						%		
Aug.	62	29	0	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0		
Sept.	81	2	5	5	5	0	0	0	0	2	0	0	0	0	0	0	0	0		
Oct.	26	5	8	13	17	5	0	0	2	16	0	2	0	0	0	4	2	0		
Nov.	29	8	2	11	13	9	4	0	0	0	0	4	13	0	0	3	2	2		
Dec.	4	54	3	4	6	8	2	3	3	4	1	0	0	1	0	1	2	4		
Jan.	4	56	2	3	7	4	1	0	0	0	2	12	5	0	0	0	4	0		
Feb.	1	52	8	8	6	3	0	0	0	0	8	5	3	0	3	1	1	1		
Mar.	16	32	5	7	6	4	6	4	0	0	3	5	0	0	0	10	2	0		
Apr.	22	30	9	19	10	2	3	0	0	1	0	1	0	0	0	2	1	0		
May	23	31	4	7	8	6	1	1	0	1	7	1	0	0	0	5	5	0		

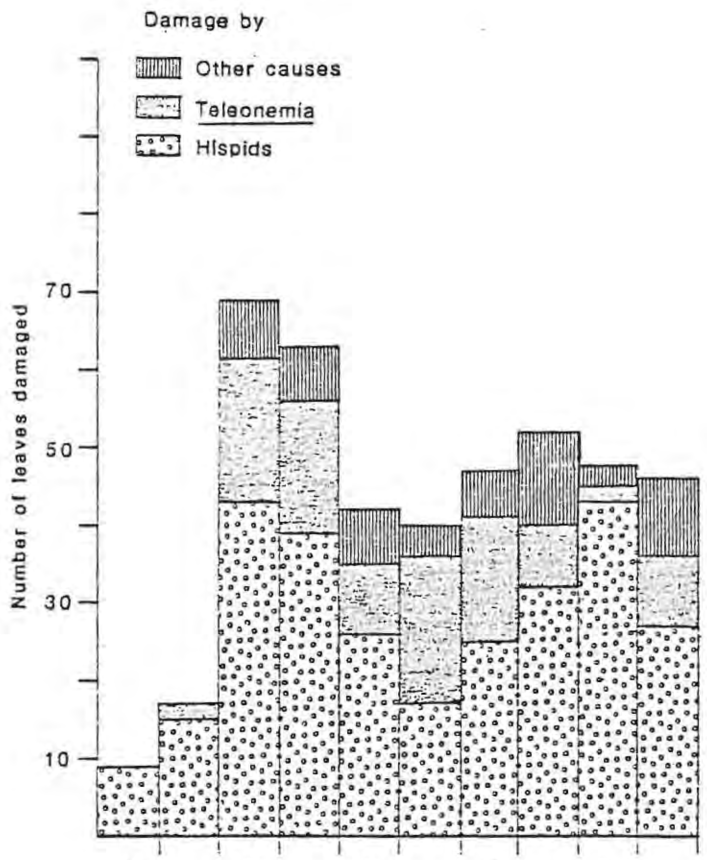

Fig. 16. Lantana camara: The number of leaves damaged per 100 leaf sites and the different causes of damage to the leaves. Destructive sampling, Margate, 1979-80.

damaged by Teleonemia were lost before leaves began to be damaged by the hispids, but whether this was so could not be ascertained.

In August-September each year the commonest leaf damage was feeding scars caused by adult hispids. From October to January the principal damage was due to feeding by adult beetles and mining by larvae. In January-February the damage was predominantly due to feeding, and to a lesser extent egg laying and larval mining, while in March - May larval mining caused most of the damage. Of leaves damaged by Teleonemia feeding scarred most leaves in December and Teleonemia-stunted leaves (following egg laying) were most common in October-November.

Leaves showing "other damage" increased towards the end of the season. Most such leaves were either tattered or had holes not caused by the hispids or by Teleonemia. This damage could have been a consequence of the weakened state of the leaves in general.

Table 8 summarizes the percentage of leaf area damaged by insects month by month during the season. The figures give a rough estimate of the reduction in photosynthetic area (compare leaf area in Table 6) for each month during the season.

Table 8: Rating for leaf damage.

Date	Rating <1%	1-10%	11-25%	26-50%	51-75%	76-100%	Total*
Aug 1979	0	1	8	0	0	0	149,5
Sept	5	7	5	0	0	0	133,5
Oct	10	33	19	7	0	0	799,5
Nov	2	14	15	15	17	0	1 990,00
Dec	6	9	9	12	2	4	1 151,5
Jan 1980	2	3	13	16	6	0	1 238,5
Feb	11	9	15	9	3	0	861,5
March	5	17	11	9	6	4	1 368,5
April	9	22	11	3	3	0	631,0
May	4	13	20	7	1	1	852,5

The pie diagram below (Fig. 17) shows that although the proportion of damaged leaves fell, the proportion of lost leaves rose, so that the overall result was a progressive rise in leaf damage.

*Total : e.g. 149,5 = (1 x 5,5)+(8 x 18) = Frequency x median

Fig. 17. Lantana camara: Leaf damage over three seasons. Destructive sampling, Margate, 1977-80.

Flower and Seed Production

Because Teleonemia attacks flowers and flower-buds, these were counted in the monthly samples. Flower production is reflected in seed production, so the numbers of seed-heads and of berries on the seed-heads were also recorded. The results of these observations are given in Table 9.

Table 9: *Lantana camara:* Flowers, seed-heads and berries on samples of 25 branches. Destructive sampling, Margate, 1977–80.

	Live flowers				Dead flowers				Seeds			
	a	b	c	d	a	b	c	d	Ygsh	Gsh	Rsh	Dsh
Sept.	14	4		5								1
Nov.	58	6	1	3					1	10(108)		5
Dec.	47	26	5	11	8	2				35(203)	1(8)	
Jan.	23	5			117	5	2			20(5)	5(4)	56
Feb.	8				7	3				8(12)		35
Mar.	7	1		1	6				2	6(0)		
Apr.	25	15			13					29(91)		14
Jun.	7			1	13				2	19(67)	9(17)	7
Aug.	0									1(1)	4(13)	
Sept.	2										5(4)	
Oct.	5									1(14)		
Nov.	87	29	10	12					9	17(118)		
Dec.	12	18	3	1					11	54(319)	2(11)	5
Jan.	2				11	9	6			31(28)	24(100)	55
Feb.	3	7			55	10				2(0)	13(74)	68
Mar.	25	17	14	14	23				6	11(50)	10(28)	50
Apr.	19	3			14				2	56(298)	14(76)	71
May.	3	10	1	7	6				5	30(362)	23(60)	44
Aug.	32	2	2	0	0				0	0(0)	52(108)	80
Sept.	2	1	0	11	4				3	0(0)	22(53)	18
Oct.	20	28	11	12	0	1			10	19(67)	23(44)	13
Nov.	22	12	6	13	7				7	57(171)	3(5)	38
Dec.	24	7	2	0	10				0	24(8)	5(26)	24
Jan.	8	1	1	0	57	1			0	15(0)	3(8)	63
Feb.	21	21	18	3	16	1			0	2(0)	0	40
Mar.	31	7	7	1	27				1	10(22)	11(19)	77
Apr.	1	0	0	0	10	1			5	32(184)	8(11)	13
May.	10	6	4	4	11				1	21(58)	17(87)	39

a – green flower-bud
b – flower-bud showing first colour
c – first ring of flowers open
d – full flower

Gsh – green seed-head (green berries)
Rsh – ripe seed-head (ripe berries)
Dsh – dried seed-head
Ygsh – young green seed-head with berries just starting to develop

Although L. camara flowers throughout the year, at least three major flowering periods can be distinguished; they occur in early spring, midsummer and early autumn. Production of seed-heads and berries follows closely after the flowering peaks. From Table 9 it is deducted that very few of the young flower-buds (category a) reach maturity or turn into flowers or give rise to berries. The large number of dead flower buds (category a) in January each year coincided with large numbers of Teleonemia. The number of berries per seed-head in Table 9 is not the number of berries produced, as those that dropped off either prematurely or when ripe could not be counted. The "dried seed heads" (Dsh in Table 9) could be either seed-heads that were dry after berries had dropped off or dry flower stalks (category c or d), but the high numbers of dry stalks (Dsh) in January and February closely correlated with high Teleonemia numbers. In general the flower and seed production at Margate was much lower than was observed at other sites where insect pressure was far less or absent. The effect of insects on flower and seed production will be evaluated in the next section.

6. RESULTS OF INSECT EXCLUSION EXPERIMENTS

A. Experiments at Margate.

From the destructive sampling described earlier, the population trends of the three imported insects could be followed and also the amount of defoliation, number of leaves damaged and amount of flower and seed production. All these measurements show that the insects are injurious to lantana, but they do not show how much injury was being caused because no comparisons were made with plants uncolonized by insects. This omission was remedied in the experiments now to be described. Observations were made of lantana bushes kept "free of insects" by application of an insecticide (see Materials and Methods) and of other bushes where insects were allowed to build up. The bushes kept "free of insects" in fact supported low numbers of insects at the beginning of the season, but these were soon killed off by the insecticide. It is in this special sense that the term "free of insects" is used.

From subsequent observations (i - vi below) a better idea was gained of the value of the three insects for the biological control of L. camara.

Because the experimental bushes began to put on new growth in October 1978, the observations were started on 25 October (day 0). They ended on 8 May 1979 (day 195).

(i) The records of live and lost leaves on marked branches enabled leaf lifespans to be estimated. From the data in Tables 10 & 11, the number of new-grown leaves added to the population (NGL) and the number of leaves lost (LOL) at each sampling date were calculated (see Materials and Methods). Polynomial regressions (Appendix 5) were fitted to these data, and expected NGL's and LOL's (Table 12) were calculated from the regressions. The data in Table 12 are shown as a graph in Fig. 18, from which leaf lifespans can

Table 10: *Lantana camara:* Live leaves (LL) and lost leaves (LOL) on samples of 20 marked branches and their side shoots kept free of hispids and *Teleonemia* and samples of 20 colonized by hispids and *Teleonemia.* Margate insecticidal exclusion experiment, 1978–79.

	Date	Main branches		Side shoots		Whole sample	
		LL	LOL	LL	LOL	LL	LOL
Kept free of insects	78.10.25	202	4	0	0	202	4
	78.11.23	271	25	24	0	295	25
	78.12.19	268	120	65	7	333	127
	79.01.17	256	216	109	7	365	223
	79.02.15	251	240	185	31	436	271
	79.03.15	221	305	284	76	505	381
	79.04.10	167	375	372	90	539	465
	79.05.08	140	420	378	160	518	580
Colonized by insects	78.10.25	200	15	4	2	204	17
	78.11.23	217	83	20	2	237	85
	78.12.19	69	293	107	83	176	376
	79.01.17	0	374	0	240	0	614
	79.02.15	0	390	4	254	4	644
	79.03.15	0	390	94	290	94	680
	79.04.10	0	402	146	384	146	786
	79.05.08	0	402	143	415	143	817

Table 11: *Lantana camara:* New-grown leaves (NGL) and lost leaves (LOL) on samples of 20 marked branches and their side shoots kept free of hispids and *Teleonemia* and samples of 20 colonized by hispids and *Teleonemia.* Margate insecticidal exclusion experiment, 1978–79.

	Day	Main branches				Side shoots				Whole sample			
		NGL	CNGL*	LOL	CLOL*	NGL	CNGL*	LOL	CLOL*	NGL	CNGL*	LOL	CNGL*
Kept free of insects	0**		202		4		0		0		202		4
	29	90	292	21	25	24	24	0	0	114	316	21	25
	55	92	384	95	120	48	72	7	7	140	456	102	127
	84	84	468	96	216	44	116	0	7	128	584	96	223
	113	19	487	24	240	100	216	24	31	119	703	48	271
	140	35	522	65	305	144	360	45	76	179	882	110	381
	167	16	538	70	375	102	462	14	90	118	1000	84	465
	195	18	556	45	420	76	538	70	160	94	1094	115	580
Colonized by insects	0**		200		15		4		2		204		17
	29	85	285	68	83	16	20	0	2	101	305	68	85
	55	62	347	210	293	168	188	81	83	230	535	291	376
	84	12	359	81	374	50	238	157	240	62	597	238	614
	113	16	375	16	390	18	256	14	254	34	631	30	644
	140	0	375	0	390	126	382	36	290	126	757	36	680
	167	12	387	12	402	146	528	94	384	158	915	106	786
	195	0	387	0	402	28	556	31	415	28	943	31	817

* CNGL – cumulative new-grown leaves;
CLOL – cumulative lost leaves

** First day of observations counted as day 0

Table 12: *Lantana camara:* New-grown leaves (NGL) and leaves lost (LOL) on samples of 20 marked branches and their side shoots kept free of hispids and *Teleonemia* and samples of 20 colonized by hispids and *Teleonemia.* Margate insecticidal exclusion experiment, 1978–79.

	Day	Main branches		Side shoots		Whole sample	
		NGL	LOL	NGL	LOL	NGL	LOL
Kept free of insects	0*	205	0**	0	0**	197	0**
	10	242	19	2	0	244	0
	20	276	41	15	0	291	28
	30	309	63	29	0	338	58
	40	339	86	46	0	386	88
	50	368	108	65	0	433	118
	60	394	131	87	2	480	149
	70	418	153	110	5	528	179
	80	440	175	135	11	575	209
	90	461	198	162	17	622	238
	100	479	220	191	24	669	269
	110	495	243	223	33	717	299
	120	508	265	256	43	764	329
	130	520	287	291	54	811	359
	140	530	310	329	66	859	389
	150	538	332	368	80	906	419
	160	543	354	410	95	953	449
	170	547	377	453	111	1000	479
	180	549	399	499	128	1048	510
	190	548	422	546	146	1095	540
Colonized by insects	0	204	4	0**	0**	242	0**
	10	238	58	12	7	280	58
	20	268	108	42	30	318	135
	30	293	155	72	53	356	208
	40	314	198	102	77	394	276
	50	331	237	131	100	432	341
	60	345	272	161	123	470	401
	70	356	304	191	146	508	457
	80	364	337	221	169	547	509
	90	369	356	251	193	585	557
	100	373	376	281	216	623	600
	110	376	393	311	239	661	640
	120	377	405	341	262	699	675
	130	378	414	370	286	737	706
	140	378	420	400	309	775	733
	150	378	421	430	332	813	756
	160	379	419	460	355	851	774
	170	381	413	490	379	889	789
	180	383	403	520	402	928	799
	190	388	390	550	425	966	806

* First day of observations counted as day 0

** Negative values not shown in Fig. 13.

be read off, in days, by measuring the horizontal distance between the NGL and LOL lines (see Fig. 19 for an example). Whenever LOL exceeds NGL the lifespan cannot be determined for obvious reasons (Fig. 18, C to D).

Lifespans read off from an enlarged version of Fig. 18 are tabulated in Table 13. On bushes kept free of insects, the lifespan of leaves on both main branches and side shoots gradually lengthened as the season progressed, and on average was about 4 times longer than on bushes colonized by insects (Table 13). On the latter, the leaf lifespan gradually shortened on the main branches and gradually lengthened on the side shoots as the season progressed. The difference between branches and shoots is due to (a) the growth habit of the plant: leaves are put out first on the main branches, and only when they become mature are side shoots put out; (b) insect attack: this naturally begins on the leaves first available, i.e. those on the main branches.

(ii) To explain the difference in lifespan between leaves from bushes free of insects and those from bushes colonized by insects, it is necessary to consider the numbers of insects on the plants and relate them to the numbers of damaged and lost leaves. The numbers of insects on the branches colonized by insects are given in Table 14. By December, no insects remained on bushes kept free of insects because they had all been killed by the insecticide applications. Insect damage to the leaves on these bushes was negligible in October-December. On the branches from bushes colonized by insects there was no infestation of hispids after January because there were no leaves on the main branches and those on the side shoots were too young for the beetles to oviposit in; Teleonemia numbers were low in February because of the absence of leaves on which to feed or lay eggs.

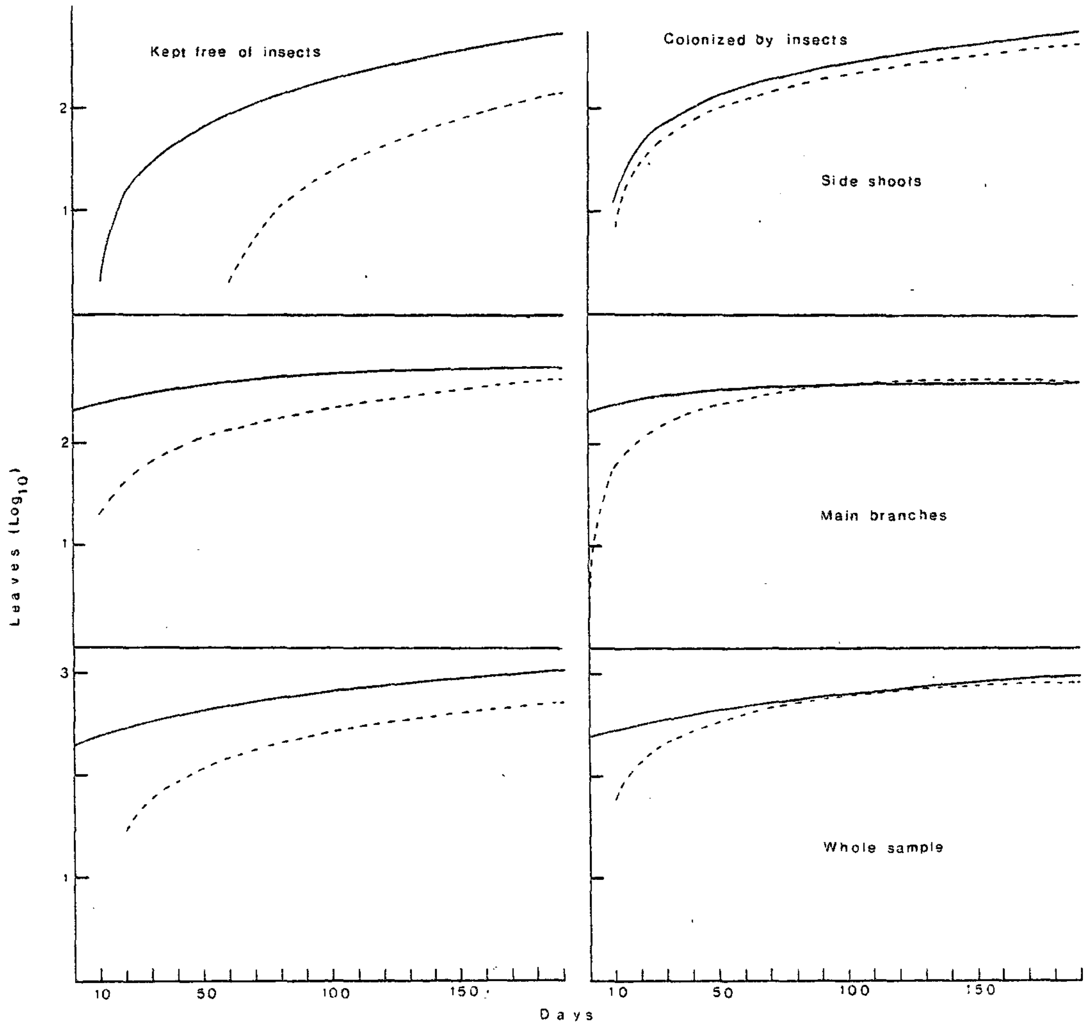

Fig. 18. Lantana camara: New grown leaves — and lost leaves -- on samples of marked branches and their side shoots. Insecticidal exclusion experiment, Margate, 1978-79.

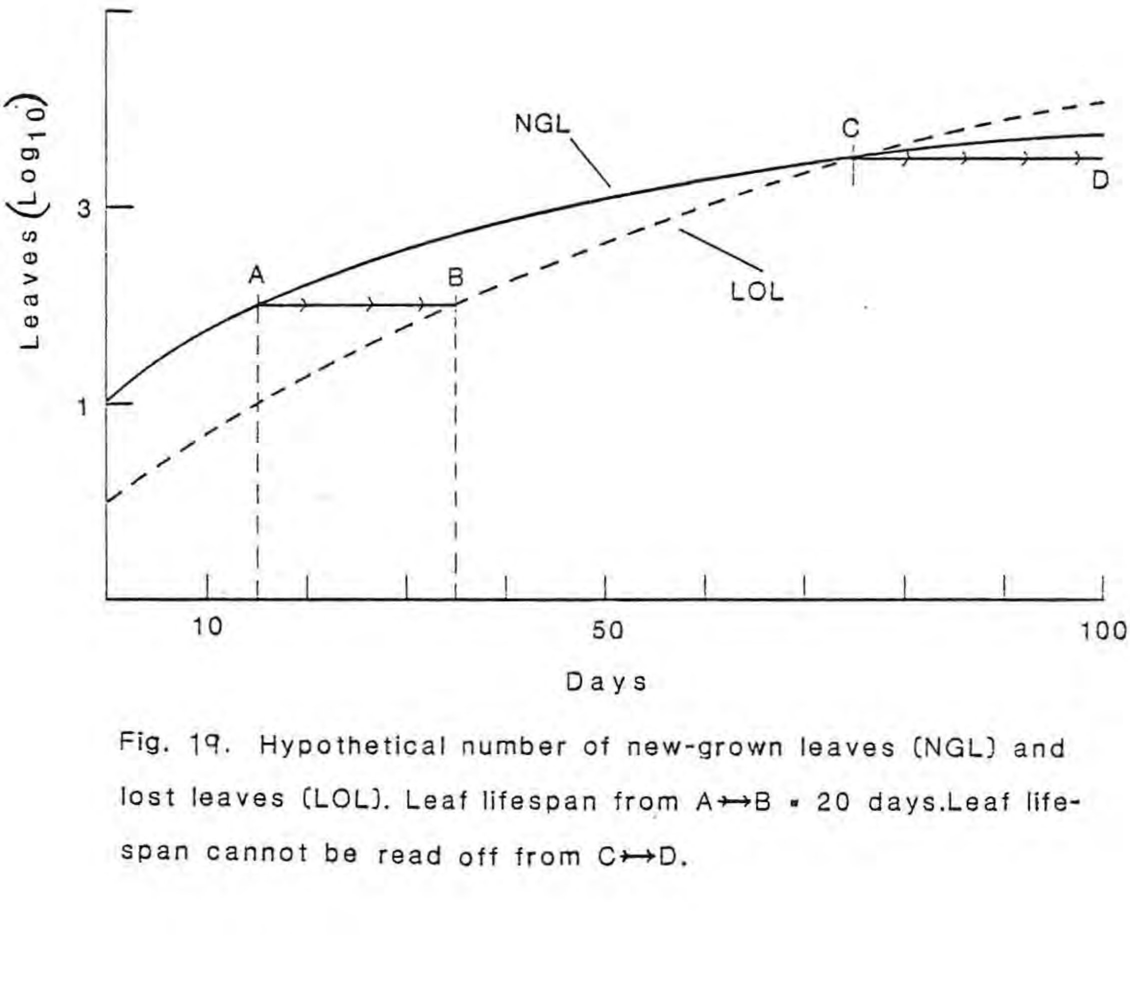

Fig. 19. Hypothetical number of new-grown leaves (NGL) and lost leaves (LOL). Leaf lifespan from A↦B = 20 days. Leaf lifespan cannot be read off from C↦D.

Table 13: *Lantana camara:* Leaf lifespans (days) on samples 20 marked branches and their side shoots kept free of hispids and *Teleonemia* and samples of 20 colonized by hispids and *Teleonemia.* Margate insecticidal exclusion experiment, 1978–79.

	Days	Main branches	Side shoots	Whole sample
Kept free of insects	0	94		74
	10	99	50	81
	20	104	66	87
	30	108	76	92
	40	112	82	100
	50	114	89	105
	60	116	95	110
	70	114	99	110
	80	110	104	759
		971	661	
		$\overline{x}$ = 107,9	$\overline{x}$ = 82,6	$\overline{x}$ = 94,9
Colonized by insects	0	41		35
	10	41	3	31
	20	39	5	28
	30	38	9	25
	40	33	11	20
	50	27	14	17
	60	21	18	11
	70	16	18	10
	80	13	19	8
	90	6	24	9
	100	0	27	5
	110		29	5
	120		32	4
	130		32	20
	140		34	40
	150		34	268
		275	309	
		$\overline{x}$ = 25	$\overline{x}$ = 20,6	$\overline{x}$ = 19,4

Table 14: *Lantana camara:* Insect numbers and damaged leaves on samples of 20 marked branches and their side shoots colonized by hispids and *Teleonemia*. Margate insecticidal exclusion experiment, 1978–79.

		Main branches									Side shoots								
	Date	Live leaves	Leaves with eggs	Total eggs	Leaves with larvae	Total larvae	Leaves with vacated mines	Leaves with feeding scars	Total leaves damaged	Total stages	Live leaves	Leaves with eggs	Total eggs	Leaves with larvae	Total larvae	Leaves with vacated mines	Leaves with feeding scars	Total leaves damaged	Total stages
Hispids	Oct.	200	18	58	5	6	0	1	24	64	4								
	Nov.	217	13	27	87	93	2	2	104	120	20								
	Dec.	69	0	0	4	6	1	1	7	6	107								
	Jan.	0									0								
	Feb.	0									4								
	Mar.	0									94								
	Apr.	0									146								
	May	0									143								

		Main branches								Side shoots							
	Date	Live leaves	Leaves with eggs	Total eggs	Total nymphs	Total adults	Total leaves with feeding	Total leaves damaged	Total stages	Live leaves	Leaves with eggs	Total eggs*	Total nymphs	Total adults	Total leaves with feeding	Total leaves damaged	Total stages
Teleonemia	Oct.	200	15	330*	54	16	31	46	400	4							
	Nov.	217	62	1364	46	30	64	126	1440	20	4	88	3	3	7	11	
	Dec.	69	3	66	92	66	38	41	224	107	35	770	187	60	65	100	1017
	Jan.	0	0	0	6	8	0	0	14	0	0	0	3	5	0	0	8
	Feb.	0			1	1			2	4	0	0	0	0	0	0	0
	Mar.	0								94	2	44	62	5	23	25	111
	Apr.	0								146	2	44	0	0	9	11	44
	May	0								143	0	0	0	0	0	0	0

*On average, each egg batch contains 22 eggs so that the number of eggs recorded for *T. scrupulosa* is the product of the leaf number multiplied by 22.

The data summarized in Fig. 20 (from Table 14) show that most leaf damage was caused by Teleonemia. This finding apparently conflicts with the conclusion from destructive sampling that most leaf damage was caused by hispids. But the comparison is misleading, because in this experiment the total defoliation of the plants in January precluded further damage by the hispids.

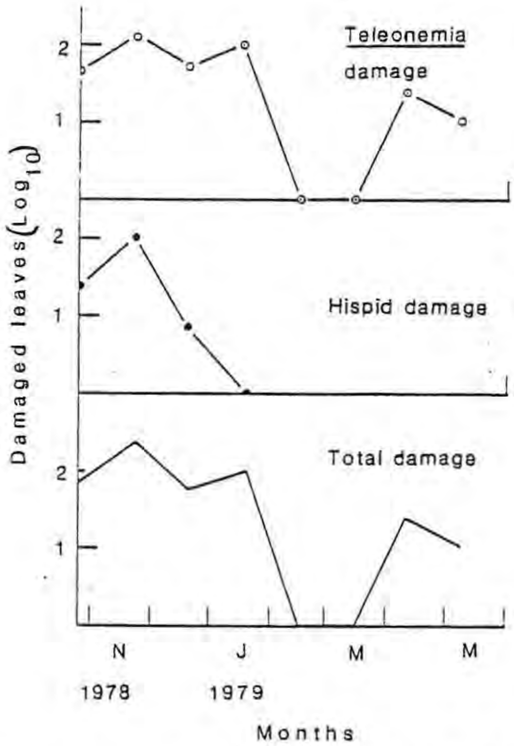

Fig. 20: Lantana camara: Leaves showing hispid and Teleonemia damage on samples of marked branches and their side shoots colonized by hispids and Teleonemia. Insecticidal exclusion experiment,Margate, 1978-79.

The numbers of live leaves (LL) and lost leaves (LOL) are given in Table 10 and shown as a graph in Fig. 21.

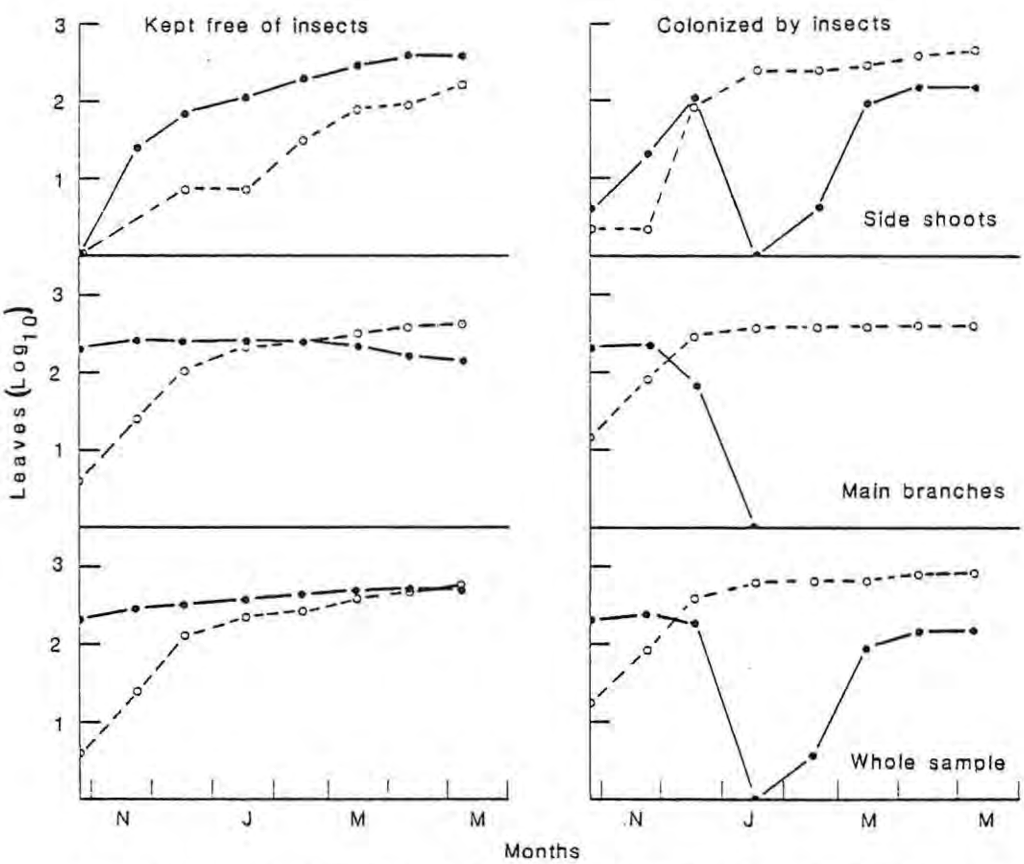

Fig. 21: Lantana camara: Live leaves ●—● and lost leaves o--o on samples of marked branches and their side shoots. Insects: Hispids and Teleonemia. Insecticidal exclusion experiment,Margate,1978-79.

On bushes colonized by insects, the main branches were completely defoliated by January and remained so. The side shoots, too, were completely defoliated by January, but later produced new leaves. On bushes free from insects, the main branches did not begin to lose leaves until February, and this was merely the natural shedding of senescent leaves at the end of summer. Figs. 22 & 23 show the difference in appearance between bushes kept free of insects and those colonized by insects.

Fig. 22. General appearance of bushes kept free of insects at Margate, January 1979.

Fig. 23. General appearance of bushes colonized by insects at Margate, January, 1979.

To sum up, the results show that on bushes colonized by insects the number of leaves was progressively reduced (as a consequence of their increasingly shortened lifespan) to the point of severe defoliation from January onwards, whereas on bushes kept free of insects the number of leaves rose steadily until the end of summer.

(iii) The total leaf area rose in summer and fell gradually in autumn on the main branches of bushes kept free of insects, but rose continuously on the side shoots. It reached over 1 300 cm^2 and over 4 300 cm^2, respectively, in May (Table 15). On bushes colonized by insects the picture was strikingly different. Total leaf area fell to zero on the main branches (because they lost all their leaves) and reached only about 640 cm^2 on side shoots in May after falling to zero in January. Similar contrasts were observed in the mean numbers of leaves/branch and in the mean leaf sizes (Table 15).

(iv) On bushes free of insects the mean diameter of main branches nearly doubled by the end of the season, but on bushes colonized by insects it increased only 1,3 times (Table 16). The total numbers of internodes on main branches plus side shoots increased 5,1 and 4,3 times, respectively, and the total branch lengths increased 8,5 and 2,5 times. Also, internodes were fewer and shorter on branches from colonized bushes (Table 16).

(v) Insect attack led to the death of some main branches and side shoots (Table 17), which partly accounts for the very low leaf production already mentioned (cf. Tables 10 & 14). The internodes started to die in December and January on main branches and side shoots that had lost all their leaves owing to insect attack. Also, the number and total length of internodes that died on such plants greatly exceeded the number and total length of internodes that died on plants kept free of insects (Table 17).

Table 15: *Lantana camara:* Total live leaves (LL), total leaf area (cm^2) (LA) and leaf area per 100 live leaves (LA/100) of leaves on samples of 20 marked branches and their side shoots kept free of hispids and and *Teleonemia* and samples of 20 colonized by hispids and *Teleonemia.* Margate insecticidal exclusion experiment, 1978–79.

		Main branches					Side shoots				
	Date	LL	LA	LA/100	Leaves/ branch	Mean leaf area	LL	LA	LA/100	Leaves/ branch	Mean leaf area
Kept free of insects	Oct.	202	1832	907	10	9,1	0	0	0	0	0
	Nov.	271	3336	1231	14	12,3	24	121	504	3	5,0
	Dec.	268	4441	1657	13	16,6	65	531	817	5	8,2
	Jan.	256	4493	1755	13	17,6	109	1062	974	7	9,7
	Feb.	251	3543	1412	13	14,1	185	1768	956	7	9,6
	Mar.	221	2988	1352	11	13,5	284	2908	1024	5	10,2
	Apr.	167	1945	1165	8	11,7	372	3798	1021	6	10,2
	May	140	1352	966	7	9,7	378	4341	1148	5	11,5
Colonized by insects	Oct.	200	1795	898	10	9,0	4	32	800	4	8,0
	Nov.	217	2548	1174	11	11,7	20	146	730	7	7,3
	Dec.	69	398	577	4	5,8	107	343	321	4	3,2
	Jan.	0	0	0	0	0	0	0	0	0	0
	Feb.						4	20	500	0,1	5,0
	Mar.						94	367	390	2	3,9
	Apr.						146	429	294	2	2,9
	May						143	639	447	2	4,5

Table 16: *Lantana camara:* Average stem diameter (mm), total number of internodes, total branch length (mm), and number of side shoots on samples of 20 marked branches and their side shoots kept free of hispids and *Teleonemia* and samples of 20 colonized by hispids and *Teleonemia*. Margate insecticidal exclusion experiment, 1978–79.

		Main branches			Side shoots			
	Date	Mean diameter	Number of internodes	Total branch length	Number of shoots	Mean diameter	Number of internodes	Total shoot length
Kept free of insects	Oct.	2,3	105	1174	0	0	0	0
	Nov.	2,8	143	2881	7	1,3	12	130
	Dec.	3,4	187	3761	13	1,4	36	457
	Jan.	3,4	214	4017	16	1,8	49	802
	Feb.	4,1	244	4423	28	1,7	101	1379
	Mar.	4,6	257	4632	53	1,5	147	2332
	Apr.	4,6	266	4807	62	1,6	216	3735
	May	4,7	274	4942	71	1,7	264	5041
Colonized by insects	Oct.	2,3	110	1592	1	1,5	3	25
	Nov.	2,9	146	2461	3	1,5	11	117
	Dec.	3,0	172	2889	31	1,4	93	733
	Jan.	3,2	189	2991	34	1,4	110	812
	Feb.	3,4	195	3052	35	1,4	130	878
	Mar.	3,6	195	3059	63	1,3	187	1107
	Apr.	3,2	201	3060	71	1,9	227	1287
	May	3,0	201	3071	75	1,8	282	1462

Table 17: *Lantana camara:* Number of and length (mm) of dead internodes on samples of 20 marked branches and their side shoots kept free of hispids and *Teleonemia* and samples of 20 colonized by hispids and *Teleonemia*. Margate insecticidal exclusion experiment, 1978–79.

	Date	Main branches		Side shoots	
		Dead internodes	Total length dead	Dead internodes	Total length
Kept free of insects	Oct.				
	Nov.				
	Dec.				
	Jan.				
	Feb.			2	27
	Mar.			6	83
	Apr.			6	83
	May	8	63	6	83
Colonized by insects	Oct.				
	Nov.				
	Dec.	3	27		
	Jan.	21	117	6	8
	Feb.	26	183	16	79
	Mar.	77	948	58	373
	Apr.	146	2237	143	740
	May	175	2539	139	756

(vi) Although there was a high mortality among small green flower buds (category a) on branches from plants kept free of insects, seed was set and ripened normally (categories Gsh and Rsh, Table 18). On plants colonized by insects, very few flower buds were produced, none reached maturity and no seeds were set (Table 18). At the end of the season the colonized bushes coppiced from the main stem and also put out new shoots from the roots.

B. Experiments at Letaba

The experiment at Letaba was basically similar to the one at Margate, but a more aggressive variety of lantana was studied and the climate was different. Combining the results from the two areas enabled firmer and broader-based conclusions to be drawn.

The climate at Letaba Estates, Tzaneen, in northern Transvaal is sub-tropical. Tzaneen is in a summer-rainfall area, and the difference between daily maximum and minimum temperatures is

Table 18: *Lantana camara:* Flowers and seed-heads (berries) production on samples of 20 marked branches and their side shoots kept free of hispids and *Teleonemia* and samples of 20 colonized by hispids and *Teleonemia*. Margate insecticidal exclusion experiment, 1978–79.

		Live flowers				Dead flowers				Seed-heads (berries)			
	Date	a*	b	c	d	a	b	c	d	Ygsh**	Gsh	Rsh	Dsh
Kept free of insects	Oct.												
	Nov.	26	9	1	1								
	Dec.	11	5	4	3	11	4	1	1	8	34(306)		
	Jan.	3	2	2	0	22	2	2			23(141)	26(154)	23
	Feb.	0	1	0	1	16	4	2			3(1)	30(116)	21
	Mar.				6	8						1(14)	
	Apr.	2	2		1	6						2(10)	2
	May	2	7		8								1
Colonized by insects	Oct.	8									2		
	Nov.	21	4			17					9		
	Dec.	7				36					6		
	Jan.	2				4					9		
	Feb.												
	Mar.												
	Apr.	3	2										
	May	1											

*a – green flower bud
b – flower bud showing first colour
c – first flowers open
d – full flower

**Ygsh – young green seed-head
Gsh – green seed-head (number of berries)
Rsh – ripe seed-head (number of berries)
Dsh – dried seed-head

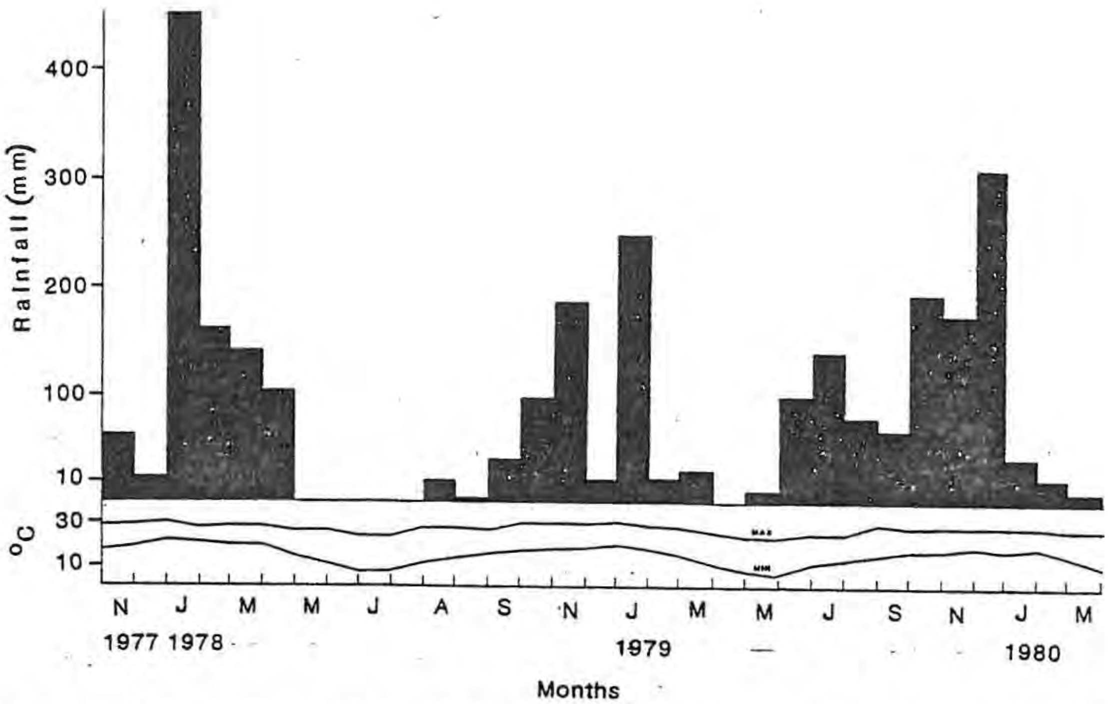

Fig. 24: Monthly rainfall (mm) and monthly maximum and minimum temperatures (°C) at Letaba, 1977-80.

greater than at Margate (Figs 13 & 24). (Data from Weather Station, Letaba Estates). The pink form of lantana that predominates at Letaba differs in leaf texture and especially in growth habit from the form that predominates at Margate and is also more aggressive - it can grow up into trees and can smother other vegetation with its dense canopy. In order to obtain data on the behaviour of this plant, pre-release studies were carried out at Letaba during 1977-79, while populations of the released insects were building up. In the event they did not build up as expected, and the "pre-release" period therefore extended to cover two seasons. During the second season (1978-79), studies were also done on lantana plants in an outdoor cage, into which all three insects were introduced in 1978, as part of the programme to culture the insects for later field releases. In this walk-in cage, commercially known as a tunnel, which was covered with shade cloth (40%) and measured approximately 30 x 8 x 5 metres, the insect populations rapidly built up.

Teleonemia reached Letaba before 1977, having originally been released 42 km from the Estate. Octotoma and Uroplata were first released during 1978 and later at intervals during 1978-81 (Table 2). In August 1977 a stand of lantana at Letaba was cut back, and by November there was enough regrowth to allow branches to be marked, at random, for observation. In August 1978 a new set of branches was marked, also at random, but arising not from the main trunks but from the main branches. Six bushes were chosen; three were exposed to full sun all day and the other three were shaded from about noon by a tree, Acacia polyacantha Willd. In both seasons 30 branches were marked, but in December 1977 two branches disappeared, and only 28 branches were studied throughout the 1977-78 season. In the 1978-79 season 20 branches were also marked in the tunnel, and the build-up of the insects and their damage to the plants were studied. As the insect numbers recorded in the field in 1977-79 were very low the effect they had on the lantana was negligible. The field bushes are regarded as controls and are referred to as "free of insects". The latter term is used in this special sense when referring to the field observations at Letaba. In the tunnel, where the insects did build up, the lantana bushes are referred to as "colonized by insects".

The data from Letaba were treated in exactly the same way as those at Margate. In essence, results confirmed those from Margate. There are some clear anomalies which relate to the fact that the insect-colonized plants were in the tunnel and an explanation is given later. The results from the experiments at Letaba are summarized in (i) - (vi) below.

(i) Fig. 25 was drawn from the data in Tables 19, 20 & 21. The polynomial regressions used to calculate the expected NGLs and LOLs in Table 21 are given in Appendix 6. The leaf lifespans are given in Table 22, read off from an enlarged version of Fig. 25. On the main branches free of insects the average leaf lifespans were 102 and 98 days, on the side shoots 96 and 95 days in 1977-78 and 1978-79 respectively.

The leaf lifespans on branches colonized by insects were far shorter and were 77 days on the main branches and 59 days on the side shoots (Table 22).

Table 19: *Lantana camara:* Live leaves (LL) and leaves lost (LOL) at Letaba on samples of marked branches and their side shoots free of hispids and *Teleonemia* (1977–79) and on samples of marked branches and their side shoots colonized by hispids and *Teleonemia* (1978–79).

	Date	Main branches		Side shoots		Total sample	
		LL	LOL	LL	LOL	LL	LOL
Free of insects	77.11.07	555	39	877	1	1432*	40
	77.12.12	664	121	2178	38	2842	159
	78.01.04	729	169	2891	164	3620	333
	78.02.07	727	321	4341	351	5068	672
	78.03.07	543	556	5698	1064	6241	1620
	78.04.18	134	998	4713	4561	4847	5559
	78.06.06	42	1108	5601	6369	5643	7477
	78.09.20	364	51	68	0	432**	51
	78.10.17	548	76	163	1	711	77
	78.11.13	610	111	256	8	866	119
	78.12.11	575	204	333	39	908	243
	79.01.09	426	411	432	122	858	533
	79.02.06	416	498	542	177	958	675
	79.03.06	234	703	455	310	689	1013
	79.04.02	107	846	250	551	357	1397
	79.05.14	40	926	48	753	88	1679
Colonized by insects	78.10.17	201	4	76	0	277***	4
	78.11.13	373	23	712	6	1085	29
	78.12.11	434	74	1327	83	1761	157
	79.01.09	440	140	2044	318	2484	458
	79.02.06	271	336	2601	1108	2872	1444
	79.03.06	157	493	3131	2486	3288	2979
	79.04.02	97	637	5891	4300	5988	4937
	79.05.14	55	683	4673	6470	4728	7153

* 28 samples of marked branches: ** 30 : *** 20.

Table 20: *Lantana camara:* New-grown leaves (NGL) and leaves lost (LOL), at Letaba, on samples of marked branches and their side shoots free of hispids and *Teleonemia* (1977–79) and on samples of marked branches and their side shoots colonized by hispids and *Teleonemia* (1978–79).

		Main branches				Side shoots				Whole sample**			
	Date	NGL	CNGL*	LOL	CLOL*	NGL	CNGL*	LOL	CLOL*	NGL	CNGL*	LOL	CLOL*
Free of insects	Nov.		555		39		877		1		1432		40
	Dec.	191	746	82	121	1338	2215	37	38	1529	2961	119	159
	Jan.	113	859	48	169	839	3054	126	164	952	3913	174	333
	Feb.	150	1009	152	321	1637	4691	187	351	1787	5700	339	672
	Mar.	51	1060	235	556	2070	6761	713	1064	2121	7821	948	1620
	Apr.	33	1093	442	998	2512	9273	3497	4561	2545	10366	3939	5559
	Jun.	18	1111	110	1108	2696	11969	1808	6369	2714	13080	1918	7477
													***
	Sept.		364		51		68		0		432		51
	Oct.	209	573	25	76	96	164	1	1	305	737	26	77
	Nov.	97	670	35	111	100	264	7	8	197	934	42	119
	Dec.	58	728	93	204	108	372	31	39	166	1100	124	243
	Jan.	58	786	207	411	182	554	83	122	240	1340	290	533
	Feb.	77	863	87	498	165	719	55	177	242	1582	142	675
	Mar.	23	886	205	703	46	765	133	310	69	1651	338	1013
	Apr.	16	902	143	846	36	801	241	551	52	1703	384	1397
	May	13	915	80	926	0	801	202	753	13	1716	282	1679
											****		
Colonized by insects	Oct.		201		4		76		0		277		4
	Nov.	191	392	19	23	642	718	6	6	833	1110	25	29
	Dec.	112	504	51	74	692	1410	77	83	804	1914	128	157
	Jan.	72	576	66	140	952	2362	235	318	1024	2938	301	458
	Feb.	27	603	196	336	1347	3709	790	1108	1374	4312	986	1444
	Mar.	43	646	157	493	1908	5617	1378	2486	1951	6263	1535	2979
	Apr.	84	730	144	637	4574	10191	1814	4300	4658	10921	1958	4937
	May	4	734	46	683	952	11143	2170	6470	956	11877	2216	7153

*CNGL – cumulative new-grown leaves
*CLOL – cumulative lost leaves

** 28 samples of marked branches; *** 30; **** 20.

Table 21: *Lantana camara:* New-grown leaves (NGL) and leaves lost (LOL), at Letaba, on samples of marked branches and their side shoots free of hispids and *Teleonemia* (1977–79) and on samples of marked branches and their side shoots colonized by hispids and *Teleonemia* (1978–79).

		Main branches		Side shoots		Whole sample	
	Day	NGL	LOL	NGL	LOL	NGL	LOL
	0*	560	0**	408	0	1026	0
	10	621	0	941	0	1594	0
	20	679	42	1473	0	2161	0
	30	733	99	2005	0	2729	0
	40	784	156	2537	0	3297	49
	50	831	213	3069	0	3864	170
	60	875	269	3601	93	4432	334
	70	914	326	4134	251	5000	540
	80	951	383	4666	450	5567	789
	90	984	440	5198	689	6135	1081
	100	1013	497	5730	969	6703	1415
	110	1039	554	6262	1289	7270	1792
	120	1061	610	6794	1650	7838	2212
	130	1080	667	7327	2052	8406	2675
	140	1095	724	7859	2494	8973	3181
	150	1107	781	8391	2977	9541	3729
	160	1115	838	8923	3501	10109	4321
	170	1119	894	9455	4065	10676	4995
	180	1120	951	9987	4670	11244	5631
	190	1117	1008	10520	5315	11812	6351
	200	1112	1065	11052	6001	12379	7113
Free of insects	210	1102	1122	11584	6728	12947	7918
	0	388	57	71	22**	447	31
	10	435	43	83	6	514	34
	20	480	39	103	0**	585	42
	30	522	44	131	0	659	57
	40	562	57	164	0	736	79
	50	600	78	203	0	814	106
	60	636	105	246	0	893	140
	70	670	139	292	0	973	179
	80	701	178	341	9	1052	225
	90	730	221	392	26	1130	278
	100	757	269	444	47	1206	336
	110	782	320	496	73	1280	401
	120	805	373	547	102	1350	471
	130	825	429	596	136	1417	548
	140	843	485	642	174	1479	631
	150	859	542	686	216	1536	721
	160	873	598	724	262	1587	816
	170	885	653	758	313	1631	918
	180	894	706	786	367	1668	1026
	190	901	757	806	426	1697	1140
	200	906	805	819	489	1717	1260
	210	909	848	823	556	1728	1387
	220	909	887	818	627	1728	1519
	230	907	920	802	702	1717	1658

Continued overleaf

Table 21: — Continued

	Day	Main branches NGL	Main branches LOL	Side shoots NGL	Side shoots LOL	Whole sample NGL	Whole sample LOL
	0	241	18	156	130	0**	0**
	10	289	0**	249	0**	0	0
	20	335	0	394	0	104	0
	30	378	0	593	0	698	0
	40	419	17	844	0	1292	0
	50	456	43	1149	0	1885	47
	60	492	78	1506	0	2479	187
	70	525	120	1917	132	3073	369
	80	556	167	2380	334	3667	595
Colonized by insects	90	583	219	2897	585	4261	863
	100	609	274	3466	887	4854	1174
	110	632	330	4089	1239	5448	1528
	120	651	386	4764	1641	6042	1925
	130	670	442	5493	2094	6636	2364
	140	685	496	6274	2596	7229	2846
	150	698	545	7109	3149	7823	3371
	160	708	590	7996	3752	8417	3938
	170	715	629	8937	4406	9010	4548
	180	720	661	9931	5109	9605	5201
	190	723	683	10977	5863	10198	5897
	200	723	696	12067	6667	10792	6635

* First day of observations counted as day 0.

** Negative values and values not shown in Fig. 20.

Table 22: *Lantana camara:* Leaf lifespans (days), at Letaba,on samples of marked branches and their side shoots kept free of hispids and *Teleonemia* (1977–79) and on samples of marked branches and their side shoots colonized by hispids and *Teleonemia* (1978–79).

	Day	Main branches	Side shoots	Whole sample
Free of insects	0	111	80	88
	10	110	89	95
	20	112	96	98
	30	113	99	101
	40	110	100	102
	50	110	102	103
	60	105	103	103
	70	104	101	100
	80	100	100	100
	90	95	96	98
	100	92	96	96
	110	86	91	1262
	120	80	1153	
		1328		
		$\bar{X}$= 102,2	$\bar{x}$= 96,1	$\bar{x}$= 97,1
	0	122	109	117
	10	122	104	117
	20	118	100	116
	30	116	99	114
	40	117	98	112
	50	114	98	110
	60	107	96	98
	70	107	95	104
	80	100	95	101
	90	100	93	98
	100	93	93	98
	110	82	91	94
	120	90	88	90
	130	78	82	82
	140	73	83	78
	150	60	1424	72
	160	60		1601
		1659		
		$\bar{x}$ = 97,6	$\bar{x}$= 94,9	$\bar{x}$= 100,1
Colonized by insects	0	94	71	34
	10	93	66	53
	20	93	63	64
	30	91	60	70
	40	85	59	71
	50	84	57	74
	60	79	56	75
	70	75	56	74
	80	75	56	74
	90	70	56	74
	100	68	56	73
	110	60	56	73
	120	60	57	70
	130	60	55	879
	140	60	56	
	150	1147	880	
		$\bar{x}$= 76,5	$\bar{x}$= 58,7	$\bar{x}$= 67,6

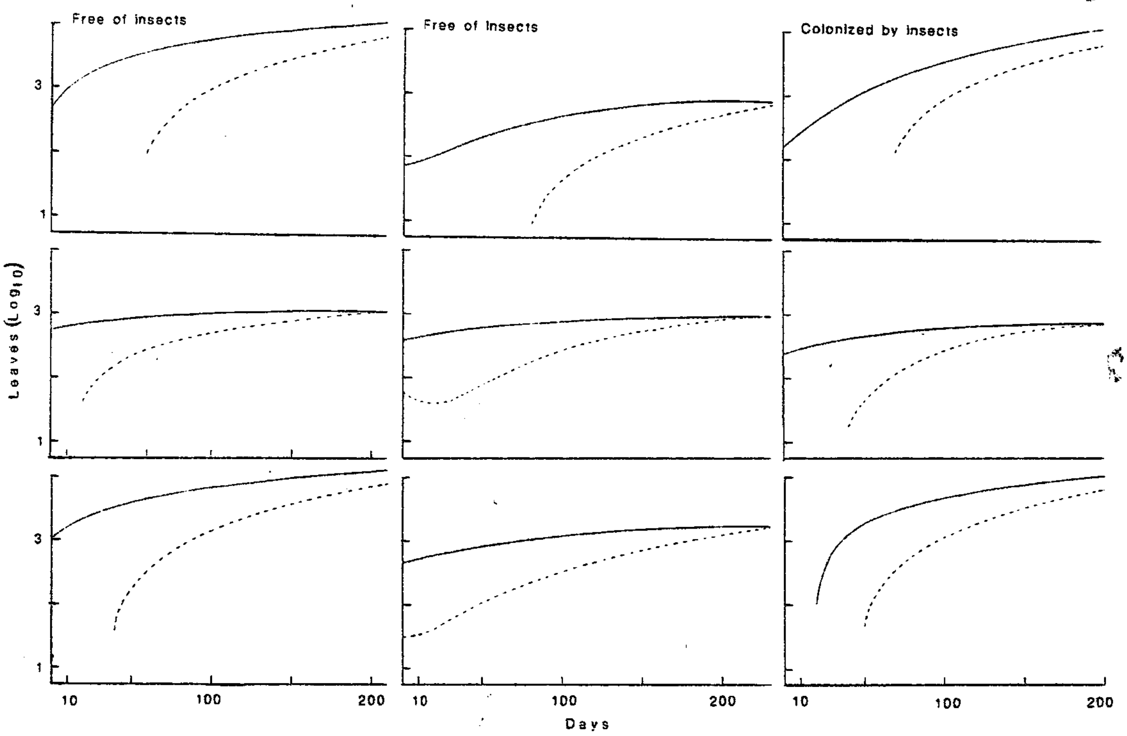

Fig. 25. Lantana camara: New-grown leaves — and lost leaves --- on samples of marked branches and their side shoots. Insects: Hispids and Teleonemia. Insect exclusion experiment,Letaba, 1978-79.

The differences in weather conditions (Fig. 24), or the fact that the marked branches were of regenerative growth in 1977-78 but not in 1978-79, had little effect on the leaf lifespans (Table 22).

(ii) Table 23 gives the numbers of insects and damaged leaves on marked branches and side shoots of bushes colonized by insects. Fig. 26 (from Table 23) records the leaf damage by the insects. Teleonemia and the two hispids caused a high level of damage from November onwards. From January onwards the main leaf damage was to leaves on the side shoots (Table 23), probably because they bore younger leaves which are preferred by the insects. The insects also caused much leaf loss (Table 19, Fig. 27). Main branches were almost completely defoliated in January-February, and leaf production on the side shoots barely kept ahead of leaf loss (Fig. 27).

On the bushes free of insects the number of live leaves on main branches declined from February to March (Fig. 27) and on the side shoots from March to April (Fig. 27). The insect damage thus caused a premature decline in numbers of live leaves (Fig. 27). The leaf loss was not as clear cut at Letaba as at Margate, probably because this was the first season of release of the insects, whereas at Margate they had been first released in 1975-76 and studied (in the work reported here) in 1978-79. Observations in the tunnel after 1978-79 have shown that the plants are now less vigorous and that more leaves are lost the longer the insects stress the plants. In 1978-79, when insects were first released in the tunnel, Uroplata outnumbered Octotoma by 2:1, but in the next two seasons Octotoma became dominant, on average outnumbering Uroplata by 55:1.

(iii) The total leaf area rose in summer and fell gradually in autumn (Table 24). The difference in number of live leaves and leaf area on branches free of insects between the two

Table 23: *Lantana camara:* Insect numbers and damaged leaves, at Letaba, on samples of marked branches and their side shoots colonized by hispids and *Teleonemia* 1978–79.

Hispids

	Main branches									Side shoots								
Date	Live leaves	Leaves with eggs	Total eggs	Leaves with larvae	Total larvae	Leaves with vacated mines	Leaves with feeding scars	Total leaves damaged	Total stages	Live leaves	Leaves with eggs	Total eggs	Leaves with larvae	Total larvae	Leaves with vacated mines	Leaves with feeding scars	Total leaves damaged	Total stages
Oct.	201						2	2		76								
Nov.	373	76	89	16	16		0	92	105	712	10	7					10	7
Dec.	434	3	6	105	373		0	108	379	1327	9	20	74	109		2	85	129
Jan.	440	0	0	60	98	75	31	166	98	2044	0	0	44	100	37	167	248	100
Feb.	271	20	87	7	12	50	58	135	99	2601	336	1062	45	75	25	524	930	1137
Mar.	157	8	15	43	87	19	40	110	102	3131	318	672	418	643	41	519	1296	1315
Apr.	97	7	13	21	33	4	33	65	46	5891	333	822	685	1117	26	1490	2534	1939
May	55	1	2	12	13	2	31	46	15	4673	27	66	182	203	59	1338	1606	269

Teleonemia

	Main branches							Side shoots							
Date	Live leaves	Leaves with eggs	Total eggs	Total nymphs	Total adults	Total leaves with feeding	Total leaves damaged	Total stages	Live leaves	Leaves with eggs	Total eggs	Total nymphs	Total adults	Total leaves with feeding	Total leaves damaged	Total stages
Oct.	201								76							
Nov.	373	36	792	2	2	5	41	796	712	35	770		2	3	38	772
Dec.	434	30	660	32	39	35	65	731	1327	25	550	35	66	119	144	651
Jan.	440	49	1078	190	101	105	154	1369	2044	97	2134	723	262	586	683	3119
Feb.	271	17	374	0	26	50	67	400	2601	62	1364	10	268	489	551	1642
Mar.	157	5	110	0	3	27	32	113	3131	23	506	4	99	913	936	609
Apr.	97	1	22	0	2	25	26	24	5891	53	1166	10	86	1139	1192	1262
May	55	1	22	0	0	7	8	22	4673	23	506	5	2	974	997	513

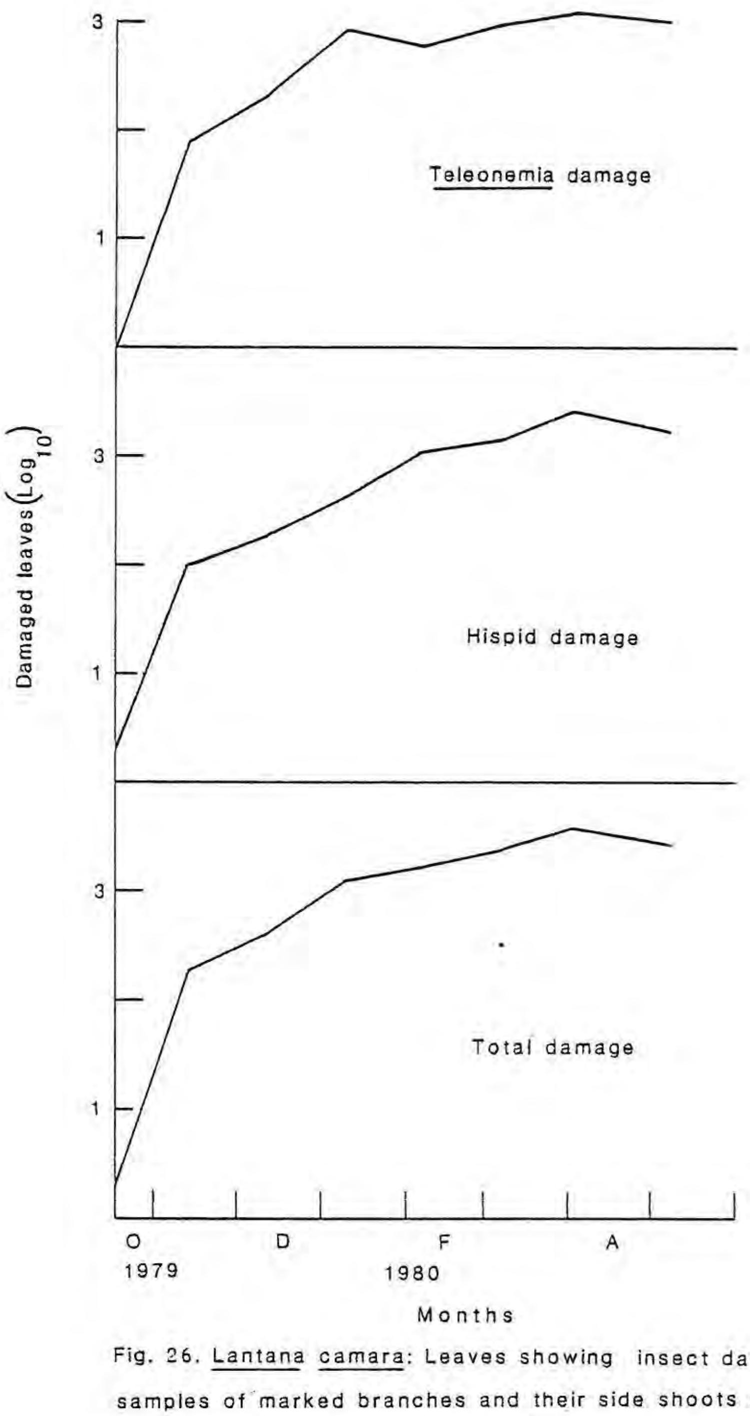

Fig. 26. Lantana camara: Leaves showing insect damage on samples of marked branches and their side shoots colonized by insects. Insects: Hispids and and Teleonemia. Insect exclusion experiment, Letaba. 1978-79.

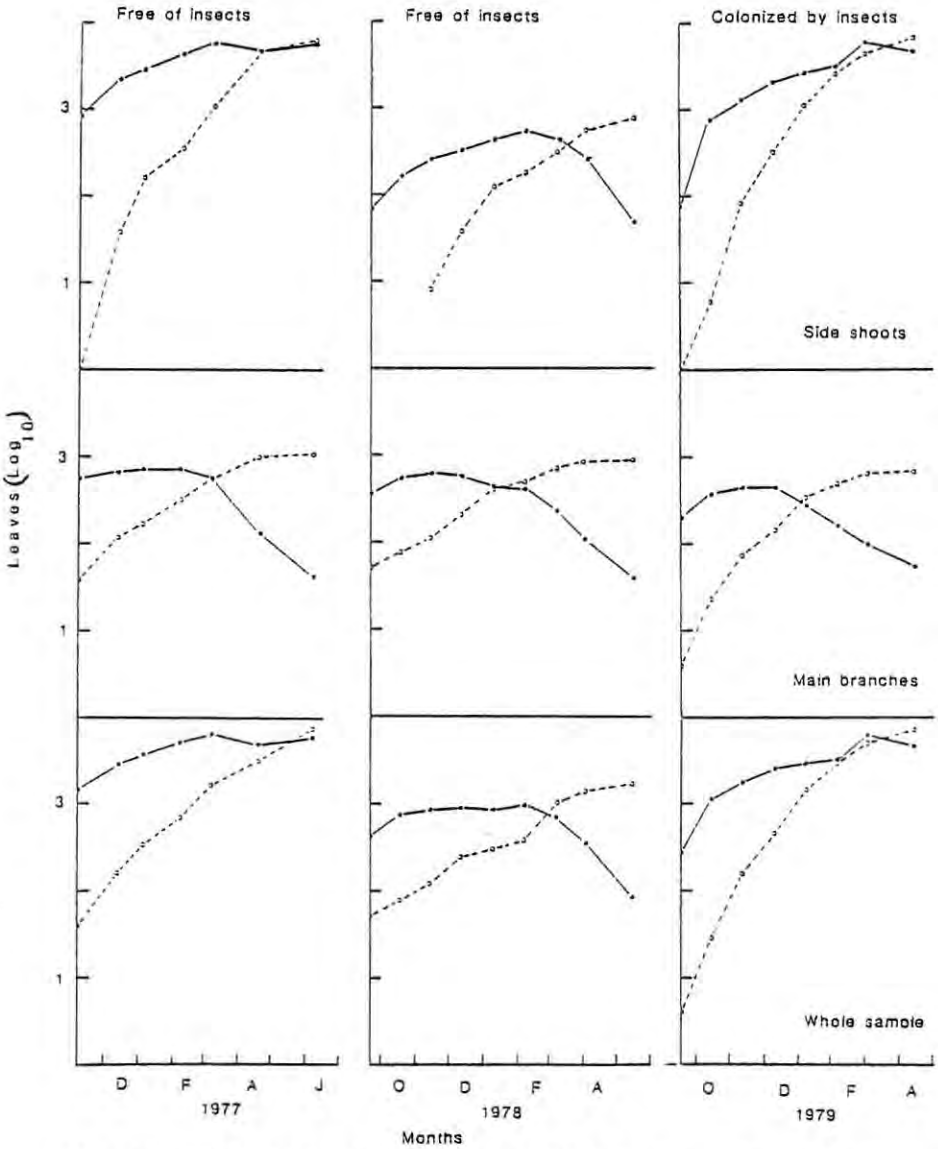

Fig. 27. Lantana camara: Live leaves •--• and lost leaves o--o on marked branches and their side shoots. Insects: Hispids and Teleonemia. Insect exclusion experiment, Letaba, 1978-97.

Table 24: *Lantana camara:* Total live leaves (LL), total leaf area (cm^2) (LA) and leaf area per 100 live leaves (LA/100) of leaves, leaves/branch, mean leaf area, at Letaba, on samples of marked branches and their side shoots, free of hispids and *Teleonemia* (1977–79) and on samples of marked branches and their sides shoots colonized by hispids and *Teleonemia* (1978–79).

		Main branches					Side shoots				
	Date	LL	LA	LA/100	Leaves/ branch	Mean leaf area	LL	LA	LA/100	Leaves/ branch	Mean leaf area
Free of insects	Nov.	555	16925	3050	20	30,5	877	14227	1622	5	16,2
	Dec.	664	23957	3608	24	36,1	2178	38882	1785	7	17,9
	Jan.	729	26863	3685	26	36,9	2891	49687	1719	8	17,2
	Feb.	727	24721	3400	26	34,0	4341	91684	2112	9	21,1
	Mar.	543	18689	3442	19	34,4	5698	115106	2020	8	20,2
	Apr.	134	4124	3078	5	30,8	4713	14994	318	5	3,2
	Jun.	142	1203	847	5	8,5	5601	89965	1606	4	16,1
	Sept.	364	3674	1009	12	10,1	432	154	36	27	0,4
	Oct.	548	4759	868	18	8,7	711	1060	149	20	1,5
	Nov.	610	7703	1263	20	12,6	866	2480	286	18	2,9
	Dec.	575	13224	2300	19	23,0	908	4386	483	16	4,8
	Jan.	426	9459	2220	14	22,2	858	5416	631	11	6,3
	Feb.	416	9988	2401	14	24,0	958	8041	839	12	8,4
	Mar.	234	6065	2592	8	25,9	689	7240	1051	8	10,5
	Apr.	107	262	245	4	2,5	357	4937	1383	4	13,8
	May	40	910	2275	1	22,8	88	680	773	1	7,7
Colonized by insects	Oct.	201	6010	2290	10,0	29,9	76	544	716	2,5	7,2
	Nov.	373	16142	4328	18,7	43,3	712	11230	1577	5,0	15,8
	Dec.	434	17941	4134	21,7	41,3	1327	26257	1979	6,2	19,8
	Jan.	440	16197	3681	22,0	36,8	2044	32104	1571	6,6	15,7
	Feb.	271	10007	3693	13,6	36,9	2601	30128	1158	5,8	11,6
	Mar.	157	5032	3205	7,9	32,1	3131	30088	961	5,0	9,6
	Apr.	97	1608	1658	4,9	16,6	5891	54515	925	5,8	9,3
	May	55	320	582	2,8	5,8	4673	25868	554	4,3	5,5

seasons is immaterial and is mainly due to the fact that smaller branches were marked the second season. On branches from bushes colonized by insects, leaf numbers and areas followed the same pattern as on those from bushes free of insects, but when insects were at their peak in December-February the leaf area was drastically reduced (Table 24).

(iv) Table 25 shows the effect of the insects on the size of main branches and their side shoots. The salient features for bushes free of insects in the two seasons 1977-78 and 1978-79 are first summarized. The mean diameter of main branches increased 1,7 times during both seasons. The number of internodes on them roughly doubled during both seasons, and their length increased 1,7 and 2,7 times respectively. The number of side shoots increased 7,4 and 5,6 times, the number of internodes on them increased about 14 and 12 times, and their length increased about 12 and 24 times.

The salient feature for bushes colonized by insects in 1978-79 are now summarized, and to facilitate comparison the corresponding figures just quoted for uninfested bushes are given in brackets. The mean diameter of main branches increased 2,4 times (1,7) the number of internodes on them increased 3,7 times (2), and their length increased 4,9 times (2,7). The number of side shoots increased 36,3 times (5,6) the internodes on them increased 145 times (12), and their length increased 198 times (24).

(v) The number and length of internodes that died on the marked branches are given in Table 26, where it can be seen that on bushes free of insects the number of internodes that died rose rapidly from March onwards. This was probably caused by shade. On branches free of insects 24% of the total internodes (24% of the total length) died in 1977-78 and 77% of the internodes (74% of the total length) died in 1978-79. On the branches with insects 48% of the total internodes (38% of the total length) died. In comparison with the branches free of insects in 1977-79, more internodes and therefore a greater length of branches died on bushes with insects.

Table 25: *Lantana camara:* Stem diameter (mm), number of internodes, total branch length (mm) on samples of marked branches and their side shoots, at Letaba, free of hispids and *Teleonemia* (1977–79) and on samples of marked branches and their side shoots colonized by hispids and *Teleonemia* (1978–79).

		Main branches			Side shoots			
	Date	Mean diameter	Number of internodes	Total length	Number of shoots	Mean diameter	Number of internodes	Total length
	Nov.	5,9	303	24447	176	1,5	427	20302
	Dec.	7,0	392	30570	313	1,9	1063	39985
	Jan.	8,4	446	33522	374	1,9	1521	54183
	Feb.	8,5	530	38371	461	2,2	2286	101865
	Mar.	9,2	558	39381	677	2,3	3335	144316
	Apr.	9,6	575	40125	960	1,9	4624	209057
Free of insects	Jun.	10,1	591	40577	1303	1,9	5970	248292
	Sept.	2,8	226	8552	16	1,4	34	638
	Oct.	3,6	303	13959	35	1,4	83	1891
	Nov.	3,7	348	16562	49	1,6	128	3228
	Des.	4,0	381	18170	57	1,5	180	5952
	Jan.	4,5	418	19641	78	1,7	266	7873
	Feb.	4,7	449	22001	80	1,7	314	12042
	Mar.	4,8	468	22742	88	1,8	376	14352
	Apr.	4,8	474	22934	89	1,8	393	15042
	May	4,8	476	22962	89	1,8	394	15117
	Oct.	3,5	101	4859	30	1,2	38	715
	Nov.	5,3	193	14071	143	1,6	336	17613
	Dec.	6,0	243	19596	215	1,9	680	32596
Colonized by insects	Jan.	6,6	283	20687	308	1,7	1124	49846
	Feb.	7,2	301	20653	446	1,7	1717	55357
	Mar.	7,6	332	20718	630	1,5	2747	67643
	Apr.	8,2	364	22250	1011	1,1	4985	118232
	May	8,3	376	23548	1089	1,4	5515	141657

Table 26: *Lantana camara:* Number and total length (mm) of dead internodes, at Letaba, on samples of marked branches and their side shoots free of hispids and *Teleonemia* (1977–79) and on samples of marked branches and their sides shoots colonized by hispids and *Teleonemia* (1978–79).

		Main branches		Side shoots	
	Date	Dead internodes	Total length	Dead internodes	Total length
Free of insects	Nov.				
	Dec.				
	Jan.			38	1409
	Feb.			71	1724
	Mar.	17	457	90	2005
	Apr.	74	4188	456	15775
	Jun.	259	13934	1343	54876
	Dec.			4	40
	Jan.	14	388	31	855
	Feb.	16	476	40	1201
	Mar.	124	5250	87	3058
	Apr.	212	11339	163	6160
	May	354	17972	312	10123
Colonized by insects	Oct.				
	Nov.			13	362
	Dec.			27	1528
	Jan.			75	3689
	Feb.			238	7548
	Mar.			393	11492
	Apr.			1059	25168
	May	21	1111	2817	62070

(vi) The flower and seed production of these marked branches are set out in Table 27.

There was a high flower-bud mortality (category a & b), but also a large number of seeds were set. On bushes colonized by insects only 34 mature flowers were recorded from March to May and no seeds were set, this corresponds to the situation at Margate, where the insect attack was heavy. Thus insect attack at Letaba also prevented seed set.

The results at Letaba differ from those at Margate because the colonized plants at the former site were inside a tunnel. The bigger leaves, increase in stem diameter, increase in internodal and total length, percentage dead internodes on the branches colonized by insects at Letaba is probably due to the absence of environmental stress to which the other marked branches were exposed in the field. It should be emphasized that this was the first season the plants in the tunnel were exposed to insect attack.

However, the insect exclusion experiments at Letaba and Margate show very clearly that the three introduced insects affect the growth and phenology of lantana in a variety of ways.

Table 27: *Lantana camara:* Flowers and seed-head (berries) production, at Letaba, on samples of marked branches and their side shoots free of hispids and *Teleonemia,* (1977–79), and on samples of marked branches and their side shoots colonized by hispids and *Teleonemia* (1978–79).

	Date	Live flowers				Dead flowers				Seed-head (berries)			
		a*	b	c	d	a	b	c	d	Ygsh**	Gsh	Rsh	Dsh
	Nov.	26	2	15	23					10	19(227)		
	Dec.	18	5	2	10	81	38	3	5	10	45(428)	57(507)	15
	Jan.	246	11		21	37	20				37(208)	41(236)	114
	Feb.	188	85	19	61	18	3			41	291(2642)	14(95)	41
	Mar.	177	40	27	6	46	4	3		18	324(3023)	233(1356)	142
	Apr.	79	9	10	11	118	7	14	39	10	39(169)	232(1209)	262
Free of insects	Jun.	21	32	3	4	81	1	4	13	6	14(91)	33(147)	31
	Sept.	2		4	8								
	Oct.	26	10	2	6						18(230)		1
	Nov.	13	19	7	14						51(673)	13(46)	2
	Dec.	2				7					37(181)	55(312)	9
	Jan.	3		4	1	10					9(81)	60(292)	29
	Feb.	4	4			3					18(110)	46(243)	21
	Mar.					5				2	9(80)	40(180)	19
	Apr.			1	1	9						21(184)	14
	May					2					1(9)	3(42)	3
	Oct.												
	Nov.												
	Dec.	1	5	2		2					3		
Colonized by insects	Jan.	4	2			17				12	3		8
	Feb.	6				41					6		
	Mar.	12		1	2	82				2	12		1
	Apr.		28	6	29	127					18		5
	May		6	1	3	10					1		58

*a — green flower bud;
b — flower bud showing colour;
c — first flowers open;
d — full flower;

**Ygsh — young green seed head;
Gsh — green seed head (green berries);
Rsh — ripe seed head (ripe berries);
Dsh — dried seed head.

7. DISCUSSION

The question "why evaluation" is often asked; when a project on the biological control of a weed is described as "successful" it is often not necessary to do evaluations on the effect natural enemies have on the plant in question. If the biological control organisms cause spectacular reductions in plant populations, as in the case of Opuntia inermis (DC.) DC. and O. stricta (Haw.) Haw. in Australia, Opuntia spp. on the Island of Santa Cruz (Dodd, 1940; Goeden & Ricker, 1980), Hypericum perforatum L. in California (Huffaker & Kennett, 1959) and Senecio jacobaea L. in California (Andres & Goeden, 1971), the commonly used photographic records of "before" and "after" the release of natural enemies are acceptable evidence and detailed evaluation is not needed or justified.

However, there is indeed a need for evaluation of the effects of the imported natural enemies on weeds where the effects are slow or subtle. It is often difficult and time-consuming to do evaluations. But, methods for assessing the ways in which insects affect the vigour of a weed can be developed and have been developed, as in the evaluation of the effect of Dactylopius austrinus De Lotto on Opuntia aurantiaca Lindley (Zimmermann, 1977); of seed and stem weevils on Tribulus terrestris L. (Kirkland & Goeden, 1978; Maddox, 1980) and of Tyria jacobaeae (L.) on Senecio jacobaea L. (Dempster & Lakhani, 1979). Regardless of how effects or achievements are measured, it is also necessary to know the pre-biocontrol situation and to gain a thorough knowledge of the weed and its natural enemies (Harris, 1980; Andres & Goeden, 1971). Only then will researchers be able to develop methods for assessing the effect of natural enemies on a weed. In the biological control of a weed, the ability of a weed to compensate (compensatory power) for any damage done to it by its natural enemies or by the interference of other plant species (inter specific plant competition), must also be taken into account.

The biological control of the weed, Lantana camara has been investigated in many countries and many observations have been made, but very little evaluation of the effects of the imported insects has been done. To me there is clearly a need for evaluation of the effects imported natural enemies have on this weed.

In the following discussion the main conclusions of a study of the effects of imported insects on L. camara as well as the published tests of the effects of four types of leaf-feeding insects are given. The following points will be discussed in the light of what has been learned from my work.

- Assessment of the methods used
- Factors limiting the distribution of the imported insects
- Possibilities of eventual control of Lantana camara in South Africa
- Should additional natural enemies be released?
- Observations or experiments to be continued.

Detailed published evaluations of the effects of the imported insects for the biological control of L. camara are few. Harley et al. (1979) made the first such evaluation in 1967-72 in S.E. Queensland. Their evaluation mainly concerned the tingid Teleonemia scrupulosa since the two hispids, Octotoma scabripennis and Uroplata girardi did not reach damaging levels at the time of their experiments. Harley et al. (1979) based their evaluation on measurements of the number of leaves showing feeding scars of the tingid and on resultant defoliation. They concluded that the common pink L. camara was resistant to attack by T. scrupulosa, but that on more susceptible varieties the insect could cause long-term damage or death in combination with drought or other stress factors. They concluded that at lower levels of attack and under favourable growing conditions plants can often compensate for damage by T. scrupulosa and do not appear to suffer permanent damage. Winder & van Emden (1980) tested the effects of four types of leaf-feeding insects on potted Lantana tiliaefolia Cham., and compared them with different amounts of artificial defoliation. They devised a damage rating based on measurements of the height of the plants, the basal stem width, the number of leaves, nodes and growing tips, and leaf area. The object was to use these experiments as part of a programme for selecting effective biological control agents for *L. camara*.

In my study the compensatory powers of *L. camara* and the inter specific plant competition have been realized, but are, however, not dealt with because the main aim was to evaluate the effect of three leaf-damaging insects (*T. scrupulosa*, *O. scabripennis* and *U. girardi*). Brief reference is made to the seedfly *Ophiomyia lantanae*.

Assessment of the methods used

The principal difficulty in evaluating the effects of the three imported leaf-damaging insects on *L. camara* is that the effects are often not immediately dramatic. On the contrary, they appear gradually and cumulatively over the years, and some of them (e.g. leaf loss) are only an intensification and/or a temporary alteration of what occurs naturally (cf. Results of destructive sampling & Results of insect exclusion experiments). It is these considerations that have dictated the approach adopted in this study. When the work was started it was evident that the best way to evaluate the different effects of the imported insects would be to monitor the growth of *L. camara* plants in South Africa before and after releasing the insects. This could reveal the results of insect attack on *L. camara*, the response of the plant and whether the stress on the plant should be increased by importing other natural enemies.

The methods I used for determining the effects of the imported insects proved valuable, but were most time-consuming. Cage experiments proved useful, but field experiments were more reliable.

The marking of branches for study was more reliable than was the cutting of a random sample of branches. Large branches arising from main branches should be marked, rather than branches arising from the trunk of the plant. There is very little difference in the final results, as was shown in the experiments at Letaba, but branches arising from the trunk "disappear" under the main canopy of the plant. Cutting of branches (destructive sampling) did not allow determination of natural leaf loss, and as most of the natural enemies of *L. camara* seem to damage leaves, it is important to ascertain natural leaf loss before any insects enhance leaf loss.

Determining leaf area is useful in indicating reduction in leaf size and reduction of total photosynthetic area, but should be coupled to area removed by insect feeding or mining. The damage rating of leaves should cover branch lengths of at least 50 cm and lost leaves should be included. This type of rating should then give indications of population growth for all insects, leaf loss and leaf damage.

The amount of damage caused to a leaf seems to determine how soon it is shed. How soon a leaf is shed due to various levels of damage, could be ascertained either in cage experiments, or with some difficulty in the field. This could be done by using the present method of determining leaf lifespans, or by starting with a cohort of marked leaves for life-table studies. Insect exclusion experiments supplemented the pre-release studies and destructive sampling. Insect exclusion experiments with insecticidal cover sprays, are not new (DeBach, 1946; Kirkland & Goeden, 1978; Harley *et al.*, 1979). However, in this study, because it was impractical to apply an insecticide every two or three weeks, a systemic insecticide, aldicarb, was incorporated in the soil once a month, with good results. Flower and seed set proved an easy way of determining the results of insect stress on the plant (cf. Results of insect exclusion experiments).

The simplest way of monitoring the effects of the natural enemies on *L. camara* would thus be to use a refined leaf damage rating to include leaf area removed by insect feeding or mining, as well as flower and seed set.

Factors limiting the distribution of the imported insects

There are two main factors limiting the spread of T. scrupulosa, O. scabripennis and U. girardi in South Africa. These factors are climate and lantana cultivars. Of the climatic factors low temperatures are a limiting factor. In areas where frost frequently occurs, e.g. Natal Coastal Hinterland, eastern Cape, Transvaal Middleveld, and western Transvaal, the T. scrupulosa numbers are drastically reduced in winter. During the hot summer in these areas, they rarely build up their numbers to levels that cause enough damage to induce severe leaf loss. In these areas the hispids also do not build up their numbers.

In subtropical areas (e.g. at Margate) where frost is rare or does not occur, T. scrupulosa populations are low at the end of winter, but rapidly increase with the advent of warmer weather. The adult hispids, which are in facultative diapause during winter, survive well in the subtropical areas.

The fact that temperature is a limiting factor corresponds with the findings of other research workers in other parts of the world (Khan, 1945; Harley & Kassulke, 1971; Harley et al., 1979). In the subtropical areas in South Africa rain has no detrimental effect on T. scrupulosa or the hispid populations (cf. Figs 13 & 24). Even in India rain only has a mechanical effect on T. scrupulosa (Khan, 1945).

T. scrupulosa shows a preference for certain specific cultivars of L. camara (Harley & Kassulke, 1971; Radunz, 1971; Harley et al., 1979). Not only is this true of L. camara in other countries, but in South Africa T. scrupulosa also shows a preference for certain cultivars of L. camara. (Botanists have yet to show whether the South African cultivars of L. camara are similar to those in other countries). Three different L. camara forms occur, for example, at Margate, La Mercy and at Shakaskraal, but T. scrupulosa only built up in numbers on the pink cultivars at Margate. At Letaba where two different pink forms occur, a similar preference to these different pink cultivars has been observed. There are indications that the hispid populations increase more rapidly on certain pink varieties and very slowly on orange cultivars, but the hispids eventually build up their numbers on all cultivars.

It is therefore concluded that T. scrupulosa and the hispids will only be of value as biological control agents of L. camara on certain cultivars in the subtropical areas of South Africa.

T. scrupulosa is already widely distributed throughout South Africa. The dominant hispid in the Natal Coastal area (e.g. at Margate) U. girardi, took three years to build up population numbers to a level where significant damage was caused to L. camara, but how long O. scabripennis, the dominant hispid in inland areas (e.g. at Letaba) will take to reach such levels, is not yet known. In Hawaii, O. scabripennis was first released in 1953. Ten years elapsed before establishment was confirmed, and since then the hispid numbers increased to levels that cause severe damage to lantana (Krauss, 1964; Davis & Krauss, 1966; Davis & Chong, 1969; Davis, 1972). In Australia the hispids became established and increased rapidly in the vicinity of several liberation sites after initial releases in 1966, 1969,1973 and have been reported to be of major importance on L. camara (Harley, 1969; 1973).

It is recommended that hispid releases be continued in new, suitable areas in South Africa for at least another five years.

Possibilities of eventual control of L. camara in South Africa

The ultimate aim of this work has been to form an opinion on whether the three imported leaf-damaging insects would be likely to control lantana within a reasonable time. The results show unequivocally that O. scabripennis, U. girardi and T. scrupulosa, acting together, reduce the vigour of two varieties of L. camara in South Africa. Moreover, the damage they caused to the plant increased annually during the three study years at Margate (cf. Fig. 17) and in the insect exclusion experiments (cf. Figs 18, 21 & 25). However, it is impossible from these results to predict or estimate how long it would take to reduce the vigour of L. camara to the point where other plants can compete with it and prevent it from spreading - or even whether this point would in fact be reached. In Hawaii the level of control of L. camara that imported insects achieved, is attributed to the greater number of similar and other insects established there (Andres & Goeden, 1971). In South Africa, T. scrupulosa, acting in conjunction with both hispids or with one of the hispids, causes extensive leaf loss on L. camara from especially December to April each year (cf. Table 7), this allows the plant to compensate in late autumn and early summer. In order to gain biological control of this weed, it is important that high levels of insect damage and subsequent excessive leaf loss be extended beyond the December - April period.

Should additional natural enemies be released?

The fact that L. camara is able to recover from the damage done to it by the three insects evaluated in the three study years, indicates that further natural enemies are needed. The great need is not only to import insects suited to ensure an extended period of damage, but to import insects suited both to temperate areas and shaded conditions e.g. in plantations.

Among the insects available for the biological control of L. camara the tingid, Leptobyrsa decora, and the cerambycid, Plagiohammus spinipennis have already been imported and released (cf. Table 2) and through the kind co-operation of CSIRO, Australia, we should be able to obtain Phytobia lantanae again, Oedionychus sp. and Aerenicopsis championi Bates as soon as these become available.

P. lantanae (Agromyzidae) is likely to do well in the subtropical areas and might supplement the three insects already established, and should be imported first. Oedionychus sp. (Halticidae), may be suited to temperate areas and should be imported as soon as it becomes available. Thereafter, the cerambycid, A. championi, should be imported, because it is generally true that cerambycids often attack plants that are already under stress.

It is known that J.A. Winder (for CSIRO, Australia) is searching in Brazil for additional insects for the biological control of L. camara. His project should be of great value to the future of the biological control of L. camara. Australian workers have already taken the initiative in investigating the possibility of using pathogens specific to L. camara. Both these projects should receive our attention, encouragement and support.

Observations or experiments to be continued

Apart from importing additional natural enemies for L. camara into South Africa, the following observations or experiments should be continued over the next five years.

(i) The observations started at the various study sites (cf. Fig. 2) should be continued once the insects have built up their numbers.

(ii) The hispids should be introduced into as many other suitable areas as possible.

(iii) The extent of the compensatory powers of L. camara needs attention.

(iv) Once L. camara is under stress, attention should be given to inter specific plant relationships.

(v) Once completed, the work of C.H. Stirton (Botanical Research Institute, Pretoria), on the cytotaxonomy and description of cultivars of the polyploid complex of L. camara, will be of great help in determining the susceptibility of the different cultivars of L. camara to imported natural enemies. His work will also identify areas where certain L. camara cultivars predominate. This will enable us to release the natural enemies on those cultivars they prefer.

(vi) There is an indication that seedfly infestation of L. camara berries raises the number of shrunken embryos in L. camara berries. Infested and uninfested berries should be germinated to determine if seedfly infestation influences germination to any significant extent.

It is finally concluded that the work presented here has shown that the three imported leaf-damaging insects are affecting the growth and vigour of L. camara in South African subtropical areas, but that additional natural enemies are needed in both subtropical and temperate areas. If we are to improve the biological control of L. camara in this country it is of vital importance that this work is continued.

8. SUMMARY

Lantana camara L. is an alien plant that has become a weed in South Africa because of its thicket-forming habit and vigorous growth, which enable it to invade veld, forests, riverbanks, roadsides, and any botanically disturbed areas. Its leaves and seeds are poisonous to livestock and man. It is estimated that *L. camara* at present infests more than 52 000 ha in South Africa and is still spreading.

Factors restricting the distribution of the plant in South Africa are rainfall, altitude and temperatures below 5°C. The main infestations occur along the subtropical eastern coast and the low-lying subtropical Transvaal Lowveld. Chemical and/or mechanical control is only partly successful. For this reason and because of the increasing costs of labour, fuel and herbicides, and the often difficult terrain infested by *L. camara*, biological control was investigated as an alternative. Of the twelve insects imported for the biological control of *L. camara*, the four that became established are dealt with in this study. The biology of the leaf-damaging species *Teleonemia scrupulosa*, *Octotoma scabripennis* and *Uroplata girardi* is described in detail. That of the seedfly *Ophiomyia lantanae* is dealt with more briefly. The effect of these imported insects on the growth and physical state of *L. camara* was studied by destructive sampling and insect exclusion experiments, of which the main results are as follows.

From destructive sampling:

1. Damage to leaves by hispids was most prominent in October-November and February-May. *Uroplata* was the predominant hispid species in the coastal area.

2. *Teleonemia* reached very high numbers in December-March and then rapidly declined.

3. Plants showed excessive leaf loss due to insects from December to March each year by January or February. The

amount of insect damage rose progressively during the study period from 1977 to 1980. There is an indication that smaller leaves were produced by L. camara under continued stress of attack by the hispids and Teleonemia.

4. Fewer flowers reached maturity and thus fewer seeds were set when lantana was under attack from the imported natural enemies.

From insect exclusion experiments:

(To facilitate comparison, results of observations on plants colonized by insects are quoted first and those for plants from which insects were excluded follow in brackets).

1. The mean number of live leaves on bushes colonized by insects was 30%/(68). The mean number of lost leaves (a measure of defoliation) was 70%/(32).

2. The mean leaf lifespan was 25 days/(108) on main branches and 21 days/(83) on side shoots.

3. The mean area per 100 live leaves was 883 cm^2/(1306) on main branches and 497 cm^2/(920) on side shoots.

4. The average increase in stem diameter during the season was 1,3/(2) times the starting diameter on main branches and 1,4/(1,4) times the starting diameter on side shoots.

5. The mean internodal length on main branches was 15 mm/(18) and on side shoots 5 mm/(19).

6. The total number of flower-buds produced was 105/(176).

7. The total number of berries produced on the seed-heads was 0/(742).

The effects of the imported insects at Letaba was in essence the same as those at Margate, but interpretation and comparison between the two sites is difficult and misleading because at Letaba the insect infested plants were grown in a "hot-house" tunnel and studied for one season only.

It is concluded that the imported insects affect the growth and physical state of *L. camara* in several different ways, listed above. These effects only become apparent after the insect populations have built up and pressure has been exerted on the plants for a number of seasons. The methods used in evaluating the effects of the imported natural enemies, factors limiting their distribution, and the prospects they offer for control of *L. camara* and work to be continued are discussed.

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10. APPENDICES

Locality: ______ Date: ______ Appendix 1: A data sheet.

SIDE SHOOTS		SEEDS														
SIDE SHOOTS		FLOWERS														
SIDE SHOOTS	TELEONEMIA	FEEDING														
SIDE SHOOTS	TELEONEMIA	ADULTS														
SIDE SHOOTS	TELEONEMIA	NYMPHS														
SIDE SHOOTS	TELEONEMIA	LEAVES WITH EGGS														
SIDE SHOOTS	HISPIDAE	FEEDING														
SIDE SHOOTS	HISPIDAE	ADULTS														
SIDE SHOOTS	HISPIDAE	MINES														
SIDE SHOOTS	HISPIDAE	EGGS														
SIDE SHOOTS		BREADTH														
SIDE SHOOTS		SHOOT & LEAVES														
MAIN BRANCHES		SEEDS														
MAIN BRANCHES		FLOWERS														
MAIN BRANCHES	TELEONEMIA	FEEDING														
MAIN BRANCHES	TELEONEMIA	ADULTS														
MAIN BRANCHES	TELEONEMIA	NYMPHS														
MAIN BRANCHES	TELEONEMIA	LEAVES WITH EGGS														
MAIN BRANCHES	HISPIDAE	FEEDING														
MAIN BRANCHES	HISPIDAE	ADULTS														
MAIN BRANCHES	HISPIDAE	MINES														
MAIN BRANCHES	HISPIDAE	EGGS														
MAIN BRANCHES		BREADTH														
MAIN BRANCHES		LEAVES														
MAIN BRANCHES		BRANCH														

Appendix 2: Table for determination of leaf area (mm^2), from leaf breadth, measurements in mm (columns = units; rows = tens).

Margate : Pink *Lantana camara*

Leaf area (tens)	Leaf breadth (units) 0	1	2	3	4	5	6	7	8	9
10	131,11	157,33	185,00	214,13	244,71	276,75	310,24	345,19	381,60	419,46
20	453,77	499,55	541,77	585,45	630,59	677,18	725,23	774,74	825,70 x	878,11
30	931,98	987,31	1044,09	1102,32	1162,01	1223,16	1285,76	1349,82	1415,33	1482,30
40	1550,73	1620,51	1691,94	1764,73	1838,98	1914,68	1991,83	2070,45	2150,51	2232,04
50	2315,01	2399,45	2485,34	2572,68	2661,48	2751,74	2843,45	2936,61	3031,23	3127,31
60	3224,84	3323,83	3424,27	3526,17	3629,53	3734,34	3840,60	3948,32	4057,50	4168,13
70	4280,21	4393,76	4508,75	4625,21	4743,11	4862,48	4983,30	5105,57	5229,30	5354,48
80	5481,12	5609,22	5738,77	5869,78	6002,24	6136,16	6271,53	6408,36	6546,64	6686,38
90	6827,58	6970,23	7114,33	7259,89	7406,91	7555,38	7705,31	7856,69	8009,53	8163,82

x A leaf measuring 28mm across, has a leaf area of 825,70mm^2

Polynomial regression: $Y = -51,0152 + 10,935x + 0,728x^2$

Appendix 3: Table for determination of leaf area (mm^2), from leaf breadth measurements in mm (Columns = units; rows = tens).

Letaba: Pink *Lantana camara*

Leaf breadth (units)

Leaf area (tens)	0	1	2	3	4	5	6	7	8	9
10	108,60	136,69	166,32	197,50	230,23	264,49	300,31	337,67	376,57	417,02
20	459,01	502,55	547,63	594,25	642,42	692,14	743,40	796,21	850,56^x	906,45
30	963,89	1022,87	1083,40	1145,48	1209,10	1274,26	1340,97	1409,22	1479,02	1550,36
40	1623,24	1697,68	1773,65	1851,17	1930,24	2010,85	2093,00	2176,70	2261,95	2348,74
50	2437,07	2526,95	2618,37	2711,34	2805,85	2901,91	2999,51	3098,66	3199,35	3301,59
60	3405,37	3510,70	3617,57	3725,98	3835,94	3947,45	4060,50	4175,09	4291,23	4408,91
70	4528,14	4648,91	4771,23	4895,09	5020,50	5147,45	5275,95	5405,99	5537,58	5670,71
80	5805,38	5941,60	6079,37	6218,68	6359,53	6501,93	6645,88	6791,36	6938,40	7086,98
90	7237,10	7388,77	7541,98	7696,73	7853,04	8010,88	8170,27	8331,21	8493,69	8657,72

^{x} A leaf measuring 28mm across, has a leaf area of 850.56mm^2

Polynomial regression: $Y = -87,341 + 11,870x + 0,772x^2$

Appendix 4: Percentage leaf damage for 100 leaf sites.

LEAF DAMAGE

Locality: ____________________ Date: __________

____

Leaves lost: ____________________

No damage: ____________________

Hispidae	Eggs	E + Feeding	Mines	E + F + M^x	M + E	Feeding
1%						
1-10%						
11-25%						
26-50%						
51-75%						
76-100%						

Teleonemia	Eggs	Feeding	Other damage	Telonemia + Hispidae
1%				
1-10%				
11-25%				
26-50%				
51-75%				
76-100%				

^{x}E = Eggs, F = Feeding, M = Mining.

Remarks: ____________________

____

____

Appendix 5: Polynomial regressions used to calculate the expected new-grown leaves (NGL) and lost leaves (LOL) on samples of 20 marked branches and their side shoots kept free of insects and on samples of 20 marked branches and their side shoots colonized by insects. (Hispids and *Teleonemia*). Margate, insecticidal exclusion experiment, 1978 -79.

Kept free of insects

NGL on main branches	$y = 200,16 + 3,77x - 0,03x^2 + 0,00006x^3$
LOL on main branches	$y = -1,59 + 5,63x - 0,02x^2$
NGL on side shoots	$y = 8,50 - 0,77x + 0,034x^2 - 0,081x^3$
LOL on side shoots	$y = -18,70 + 2,32x$
NGL on whole sample	$y = 203,92 + 3,58 + 0,016x^2 \quad 0,000055x^3$
LOL on whole sample	$y = 31,17 + 8,35x - 0,02x^2$

Colonized by insects

NGL on main branches	$y = 201,45 + 3,79x - 0,01x^2$
LOL on main branches	$y = -6,03 + 2,24x$
NGL on side shoots	$y = -36,95 + 2,19x$
LOL on side shoots	$y = 3,85 - 0,40x + 0,006x^2$
NGL on whole sample	$y = 226,93 + 3,71x$
LOL on whole sample	$y = -34,92 + 3,008x$

Appendix 6: Polynomial regressions used to calculate the expected new-grown leaves (NGL) and lost leaves (LOL), at Letaba, on samples of marked branches and their side shoots free of insects (1977-79) and on samples of marked branches and their side shoots colonized by insects (1978-79). (Hispids and *Teleonemia*).

Free of insects

NGL on main branches	$y = 553{,}93 + 6{,}34x - 0{,}018x^2$
LOL on main branches	$y = -77{,}26 + 5{,}682x$
NGL on side shoots	$y = 355{,}16 + 53{,}22x$
LOL on side shoots	$y = 10{,}03 + 11{,}02x + 0{,}20x^2$
NGL on whole sample	$y = 969{,}38 + 56{,}77x$
LOL on whole sample	$y = 1{,}73 - 7{,}61x + 0{,}21x^2$

NGL on main branches	$y = 383{,}21 + 4{,}82x - 0{,}011x^2$
LOL on main branches	$y = 59{,}28 - 2{,}02x + 0{,}05x^2 - 0{,}000012x^3$
NGL on side shoots	$y = 69{,}92 + 0{,}74x + 0{,}44x^2 - 0{,}000014x^3$
LOL on side shoots	$y = 0{,}99 - 0{,}22x + 0{,}0023x^2 + 0{,}000052x^3$
NGL on whole sample	$y = 440{,}92 + 6{,}45x + 0{,}23x^2 - 0{,}00012x^3$
LOL on whole sample	$y = 60{,}27 - 2{,}24x + 0{,}055x^2 - 0{,}000068x^3$

Colonized by insects

NGL on main branches	$y = 236{,}35 + 4{,}97x - 0{,}013$
LOL on main branches	$y = 20{,}31 - 2{,}76x - 0{,}074x^2 - 0{,}000022x^3$
NGL on side shoots	$y = 149{,}85 + 6{,}06x + 0{,}27x^2$
LOL on side shoots	$y = -15{,}43 + 10{,}71x - 0{,}42x^2 + 0{,}0051x^3$
NGL on whole sample	$y = 677{,}68 - 25{,}82x + 0{,}74x^2 - 0{,}0017x^3$
LOL on whole sample	$y = 150{,}4 - 22{,}82x + 0{,}38x^2 - 0{,}00051x^3$

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