# BIOLOGICAL STUDIES OF INSECT HERBIVORES ASSOCIATED WITH SOME SPECIES OF *SOLANUM* L.

by

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## CONTENTS

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## ABSTRACT

1. *Solanum mauritianum* Scop. (bugweed), a serious exotic weed in South Africa, supports a depauperate herbivore fauna relative to indigenous *Solanum* species. These comprise mainly polyphagous, and some oligophagous, species.

2. The greater diversity of insect herbivores on *Solanum hermannii* Dun., relative to other indigenous *Solanum* species in the eastern Cape, suggests that the plant is indigenous and not exotic as has been suggested.

3. Five oligophagous species seasonally caused a high incidence of damage to *S.hermannii* and other indigenous *Solanum* species in the eastern Cape, during the study period.

4. Galls of the flowers, stems and leaves of some indigenous *Solanum* plants are described and biological data on the gall-formers and their natural enemies presented.

5. The tortoise beetle, *Conchyloctenia tigrina* Oliv. (Chrysomelidae), defoliates a wide range of indigenous *Solanum* species. The exotic *S.mauritianum* and *S.elaeagnifolium* Cav. were unfavourable for growth and survival. *S.hermannii* proved the most favourable of the indigenous hosts tested, for growth and survival, providing further evidence that it is indigenous.

6. Extensive studies on different field populations of the beetle revealed no evidence of host adaptation (host races). All populations tested displayed greater fitness when reared on *S.hermannii*.

7. South African *Solanum* faunas are characterized by a scarcity of endophagous and monophagous herbivores, vacant feeding niches and low numbers of species relative to other plant taxa. This may suggest evolutionary immaturity of the insect-plant associations, although comparative studies of solanums from other parts of the

world are needed for confirmation. Alternatively, these characteristics may simply be a feature of the genus *Solanum* in general.

8. The depauperate herbivore fauna of *S.mauritianum* reflects a lack of local herbivores suitably preadapted to overcome its defences. This appears to be accentuated by absence of any close relatives of bugweed in South Africa. The greater diversity of herbivores in its native South America suggests that biological control may be a potentially useful means of control for bugweed. The potential for biological control is, however, threatened by the susceptability of the cultivated eggplant (*Solanum melongena* L.) to attack by *Solanum*-feeding insects. Possible solutions to this problem are discussed.

# 1. INTRODUCTION

## 1.1. Economic importance of the genus *Solanum* L.

The Solanaceae comprises some 84 genera and almost 3500 species worldwide (D'Arcy 1979, 1986). The genus *Solanum* includes about 75% of these species (Symon 1981) and is also the genus with the greatest geographic amplitude (D'Arcy 1979). The southern hemisphere supports much of this diversity. South America is regarded as the main centre of speciation (D'Arcy 1979, Symon 1981), supporting a conservatively estimated 1000-1100 species (Hunziker 1979). Other centres of speciation include Africa with approximately 110 species (Jaeger and Hepper 1986) and Australia with 94 species (Symon 1981).

The genus *Solanum* is of major agricultural importance worldwide; *Solanum tuberosum* L. (potatoes) and *Solanum melongena* L. (bringals, eggplant) are the most important cultivated species. Potatoes are grown in all provinces in South Africa and cover some 50 000ha per year (Annecke and Moran 1982). Although brinjals are of minor economic importance in South Africa (Annecke and Moran 1982), they are widely grown elsewhere in Africa (Jaeger and Hepper 1986) and many tropical and subtropical parts of the world (Pearce and Lester 1979).

The genus *Solanum* also incorporates a number of weed species which have invaded various parts of the world. In South Africa, *Solanum* comprises 51 indigenous and 13 exotic species (Gibbs Russell *et al.* 1987). South African species are ecologically similar to Australian species, in that they often occupy disturbed sites and are rarely components of climax vegetation (Symon 1981). Consequently, approximately 40% of the South African *Solanum* flora (15 indigenous and 10 exotic species) is regarded as problem plants (Wells *et al.* 1986). Of these, *Solanum mauritianum* Scop. (bugweed, bugtree) and *Solanum elaeagnifolium* Cav. (silverleaf nightshade, satansbos) are the most serious of the exotic weeds, the former species posing the greatest threat at present.

## 1.2. *S.mauritianum* (bugweed) in South Africa.

*S.mauritianum*, a large shrub or small tree 3-4m high (Symon 1981), is indigenous to Argentina, Brazil and Uruguay, but has been introduced into Africa, Australia, India and islands of the Atlantic, Indian and Pacific oceans (Roe 1972). It was possibly first introduced to Africa, Madagascar, Mauritius and India by way of the Portuguese trade routes, Manila- Sao Paulo- Cape Town-Goa, in the early 16th century (Roe 1972, 1979). It is unclear whether these early navigators deliberately distributed this plant globally. It has been suggested that the leaves were used as substitutes for soap and toilet paper, as cleaning agents for utensils, and to ripen bannanas (Neser 1984). In Australia, *S.mauritianum* is regarded as a useful nursery shrub, since it forms a canopy under which indigenous forest is able to regenerate (see Van Dyck 1979).

Although possibly introduced to South Africa in the early 1500's, the earliest recorded specimen of *S.mauritianum* appears to have been collected in Natal by the botanist T. Cooper (Wright 1904), who collected in this area in 1862 (Gunn and Codd 1981). Numerous observations of the plant were made by the botanist J. Medley Wood, in the vicinity of towns along the Natal coast, around 1881 (Harding 1938, Anon. 1984). An examination of herbarium specimens in a branch of the Botanical Research Institute at the Albany Museum, Grahamstown, revealed specimens collected by the botanist S. Schonland near Grahamstown in 1894. Bugweed has since spread widely (Fig. 1.1) and is highly invasive where natural bush has been destroyed or plantations cut down (Byford-Jones 1981, Anon. 1984). Bugweed also invades riverine vegetation and relatively open forested stands where trees have been trimmed (Fig.1.2).

Bugweed also produces large quantities of fruit, favoured by frugivorous birds such as Rameron pigeons, which facilitates the rapid spread of the plants. Large proportions of the seed remain viable for years (Byford-Jones 1981). In Natal, the fruit is host to the Natal fruit fly (*Ceratitis rosa* Karsch) and enables the flies

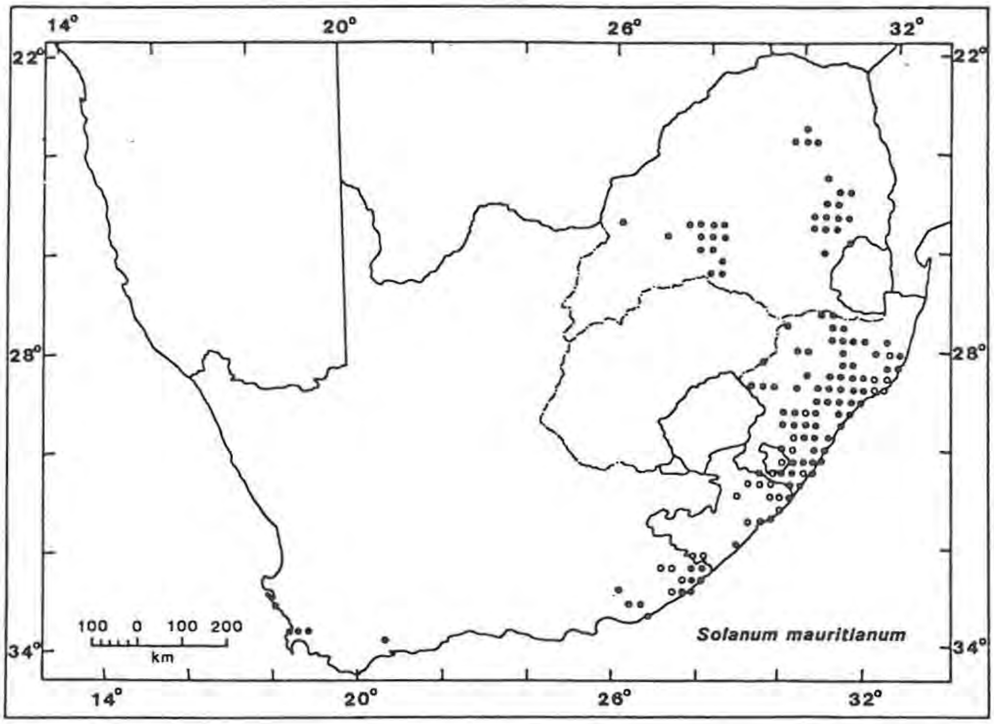

**Fig.1.1.** Distribution of *Solanum mauritianum* in South Africa. Closed circles represent records obtained from the Botanical Research Institute in Pretoria and Grahamstown and also specimens collected during the survey and identified by the BRI. Open circles represent records based on own identifications.

**Fig.1.2.** *Solanum mauritianum* infestation in a pine plantation in the Weza State Forest.

to survive over the winter (Ripley and Hepburn 1930, 1935). Bugweed is common in the eastern Cape, where it is found along watercourses, in gardens and various disturbed areas. *S.mauritianum* in South America seems to constitute a complex of forms, with many intermediates. South African forms appear closest to those encountered in northern Argentina and southern Brazil (Neser 1984).

Although *S.mauritianum* may be controlled chemically (see Byford-Jones 1981), biological control has become a high research priority in South Africa (Neser 1986). Faunistic surveys of a weed in its exotic habitat, together with surveys of related indigenous plants, can be a useful contribution to biological control (see below).

## 1.3. Faunistic surveys of *S.mauritianum* and some indigenous *Solanum* species in South Africa.

The primary aim of my research was to evaluate the diversity of phytophagous insect species on *S.mauritianum* in comparison with that of indigenous *Solanum* species. This was achieved following surveys in the eastern Cape (Chapter 3) and the Transvaal and Natal (Chapter 5). Goeden and Ricker (1986a) demonstrated the value of pre-introduction faunistic surveys during the planning of biological control campaigns. One would expect the phytophagous insect faunas to be rich on indigenous plants and depauperate on exotic species (eg. Southwood 1961, Southwood *et al.* 1982). However, insects find and colonize most species of introduced plants relatively quickly and the number of colonizing species depends in part on how widely the plants have become established (Strong *et al.* 1984). Since bugweed has become widely established in South Africa, it could be expected that it would have recruited some phytophages from the local "pool" of insects that feed on *Solanum* species. Information as to which types of phytophages (stem borers, leaf miners etc.) are lacking on bugweed in South Africa, is of importance in deciding which natural enemies to import for biological control.

## 1.4. Studies on major *Solanum* herbivores.

Another aim was to identify the more common herbivores of different *Solanum* species and examine features of their biology. These included seasonal abundance, host range, nature of herbivory and natural enemies (Chapters 4 and 6). This information can be of importance in evaluations of biological control, since potential biocontrol agents may be closely related to herbivores of congeneric indigenous plants. An important consideration is whether natural enemies of the indigenous taxa might influence the efficiency of introduced agents. Numerous cases of biotic interference with weed control, from indigenous predators and parasitoids, have been recorded, and some have prevented the establishment of potential control agents (Goeden and Louda 1976). These authors noted that predators involved were mainly polyphagous, while parasitoids often transferred from native phytophagous insects to imported agents related to them. Siebert (1975) recorded pupal parasitism, in the laboratory, of the tortoise beetle *Gratiana lutescens* Boh., imported to South Africa for the biocontrol of *S.elaeagnifolium*, by Eulophidae which parasitize *Conchyloctenia tigrina* Oliv., a local tortoise beetle of indigenous *Solanum* species.

## 1.5. Mechanisms of host plant utilization.

The mechanisms whereby insect herbivores utilize a host or range of hosts are manifested in a series of complex interactions. Two principle, and often interrelated, components are host selection by the insect and plant resistence to the insect (Beck 1965). These relationships were investigated in the laboratory using the tortoise beetle *C.tigrina*, a common defoliator of indigenous *Solanum* plants in South Africa. Tortoise beetles are also common defoliators of South American *Solanum* species and at least one species (see above) was considered as a potential control agent for *S.elaeagnifolium* in South Africa (Siebert 1975). Tortoise beetles are also easily reared in the laboratory and their larval instars easily distinguished.

The laboratory studies consisted of two main parts. The first was the examination of the biology and host range of the beetle. This included life cycle studies on three indigenous and two exotic *Solanum* hosts. These studies (Chapter 7) served to illustrate the extent to which the exotic *S.mauritianum* and *S.elaeagnifolium* were suitable as hosts, relative to indigenous plants. The second part of the study was an investigation of the fitness of two different populations of the beetle on two indigenous hosts. These studies (Chapter 8) served to illustrate whether differences in fitness between indigenous hosts (observed in Chapter 7) could be related to host adaptation by the beetles (host races) or poorer quality of some hosts relative to others. Feeding and oviposition choices were examined to determine whether optimal hosts are always selected.

## 1.6. *Solanum* herbivory relative to that of other plant taxa.

Chapter 9 presents a review of features of the insect herbivores of *Solanum* plants in South Africa. The aspects considered are the nature of the herbivore guilds (feeding niches), the extent of the host ranges of the most common herbivores and the species richness of herbivores relative to other plant taxa.

## 1.7. Prospects for biological control.

The prospects for the biological control of *S.mauritianum* in South Africa are considered (Chapter 10) in terms of the status of the weed in South Africa. Aspects discussed include its herbivore diversity, feeding damage and means of dispersal, the herbivore communities and taxonomic status of indigenous species of *Solanum* and the status of cultivated species of *Solanum*.

# 2. MATERIALS AND METHODS

## 2.1. Surveys in the eastern Cape.

Insect samples were taken opportunistically during 1985 and 1986 from *S.mauritianum* and three locally-occurring species, namely *Solanum hermannii* Dun., *Solanum rigescens* Jacq. and *Solanum coccineum* Jacq. The samples originated from various areas in the eastern Cape, but mainly in the general vicinity of Grahamstown (33°19'S, 26°32'E). Individual plants were first searched for herbivores in the field and representative parts of each taken to the laboratory for further examination. Stems were dissected for borers and the leaves searched for leaf feeders. Fruit and flowers were also collected, half of which were frozen for subsequent dissection and the remainder placed in emergence cages. Voucher specimens of unidentified insect species are lodged in the Albany Museum (Natural History), Grahamstown and many also in the National Collection of Insects, Plant Protection Research Institute, Pretoria. These species are referred to in the text and tables by means of their accession numbers (AcRh values).

## 2.2. Seasonal study of common eastern Cape herbivores.

The seasonal frequencies of the major herbivores associated with *S.mauritianum* and *S.hermannii* were evaluated at a site on the outskirts of Grahamstown (33°19'S, 26°31'E), where the two species occur together. The biology and host specificity of these herbivores was also studied. Twenty plants of each species were individually marked. Leaves, stems, fruit and flowers were sampled from these plants early in the growing season (December 1985), towards its end (March 1986) and during winter (August 1986). A branch was cut at random from each plant; the branches were dissected for borers and the leaves searched for leaf feeders. The sampling method precluded the dissection of the main stems; however, a preliminary investigation disclosed no borers in these.

Samples of 10 fruit and 20 flowers were randomly picked from each

*S.hermannii* plant while 20 fruit and 20 flowers were picked from *S.mauritianum* plants. In order to effectively sample the various insect species, half of the fruit and flower samples from each plant species were frozen for dissection, while the remainder was placed in emergence cages. The method by which particular results were obtained is indicated in the appropriate figure legends. Since the branches, leaves and fruit were variable in size, insect numbers were expressed in terms of total constant dry mass of each. Insect numbers relating to flowers were expressed per number of flowers since flowers were more uniform in size.

## 2.3. Surveys in Natal and the Transvaal.

A survey of the faunas of species of *Solanum* in Natal and Zululand was conducted during the first two weeks of December 1986. Samples were taken from *S.mauritianum* and other local species like *S.hermannii*, *S.incanum* L. and *S.panduriforme* E.Mey. Collections were made at and en route between the following places: Empangeni, Eshowe, Hluhluwe Game Park, Lake Sibaya, Mapalane Nature Reserve, Mbazwana, Mkuzi Game Park, Mtubatuba, Port Shepstone, Umhlanga Rocks and Weza. Some collections were also made in the Transkei en route to Natal (Qumbu) and in the Mkambati Nature Reserve in 1988. Individual plants were first searched for herbivores in the field and representative parts of each taken to the laboratory for further examination. Fruit and flowers were kept in emergence cages.

Collections of *S.panduriforme* and *S.incanum* were also made in Zimbabwe, mainly around Harare, during December of 1985 and 1987. These two species were also sampled in areas of the Transvaal en route to Zimbabwe and on other occasions during 1988. Transvaal collections were made at the following places: Giyani, Hazyview, Lower Sabie, Masalal, Potgietersrus, Schoemanskloof and Skukuza. *S.mauritianum* was examined at Hazyview and Schoemanskloof. Sampling was conducted in a similar fashion to that of the Natal collections. Voucher specimens of unidentified species are lodged in the collections mentioned above.

## 2.4. Studies on galls.

Flower galls from *S.hermannii* and stem galls from *S.coccineum* and *S.rigescens* were collected at various sites in the eastern Cape (Tables 6.1 and 6.2). Leaf galls from *S.panduriforme* were collected at various sites in Zululand during 1986 and the Transvaal during 1987 and 1988 (Table 6.3). The gall tissue was kept as fresh as possible by pushing the stems, leaf petioles or flower stalks into moistened "Oasis" (a highly absorbant material used to support the stems in flower arranging), in emergence cages. The gall formers and their parasitoids were subsequently reared. Numerous galls were dissected in order to observe their internal structure.

## 2.5. Biology of *C.tigrina*.

Beetle cultures were maintained in gauze topped perspex cages (30cmx30cmx30cm) at 18-25$^{o}$C and a day length of 16 hours. A freshly cut branch of *S.hermannii* upon which the beetles commonly occur in the field, was placed in a jar filled with water in each cage every 3-4 days. Egg cases were removed from the leaves and isolated in hatching trays. A sample of 50 egg cases was used to determine the hatching rate and duration of the egg stage.

In a life cycle study, newly hatched or moulted larvae were reared on *S.hermannii* leaves placed in petri-dishes of 9cm diameter. Freshly collected leaves, regularly supplied, were considered suitable for this laboratory test since healthy cultures of *C.tigrina* had been maintained on sprigs of *S.hermannii*. The duration of the larval instars and the body length and width of the head capsule of the newly moulted larvae were recorded. Body length was measured to the base of the caudal process.

Data on seasonal abundance, host range and parasitism of the beetles were obtained from field observations and samples, mainly from Grahamstown, but also from other areas in South Africa and in Zimbabwe.

## 2.6. Experiments on the host range of *C.tigrina*.

To determine the suitability of different *Solanum* hosts, beetles collected from *S.hermannii* in the field were tested on *S. rigescens*, *S.coccineum* (both indigenous), *S.hermannii* (possibly indigenous) and on exotic *S. mauritianum* and *S.elaeagnifolium*. The leaves of these species showed varying degrees of pubescence. The density of trichomes increased from *S.hermannii* through *S.rigescens*, *S.elaeagnifolium* and *S.coccineum* to *S.mauritianum*. Trichomes play a role in plant defence and have often been correlated with reduced feeding and oviposition in herbivorous insects (Levin 1973).

The survival tests were conducted in glass cylinders (10,5cm high and 8,5cm diameter) with petri dishes as floor and lid. Ventilation was provided by a gauze-covered hole in the lid. Ten first instar hatchlings were placed in each of five cylinders each containing leaves of one of the test plant species. The leaves were kept fresh by pushing the petioles into moistened "Oasis". New leaves were supplied every two to three days. The larvae were reared to the adult stage and the mortality and duration of each stage of the life cycle was recorded. The cylinders were examined twice a day to obtain as accurate a measure of the duration of the stages as possible. The precise time at which a particular instar moulted into the next was recorded as the midpoint between the time when the new instar was first observed and the time last examined. The duration of each instar was thus calculated as the difference between the calculated time of the new instar and that of the previous one. Five replicates of this experiment were carried out. Each plant was thus tested five times. Kruskal-Wallis tests were conducted to determine whether mortality and duration of the life cycle differed significantly between the host plants. Where intergroup differences were significant ($p<0,05$), pairwise comparisons were conducted using the Mann-Whitney test.

## 2.7. Experiments on the possibility of host races of *C.tigrina*.

Beetles were collected from two field populations, situated about

3,5km apart outside Grahamstown. One population was hosted by *S.hermannii* and the other by *S.rigescens*. Two separate laboratory cultures were maintained under the same conditions as in the previous experiment (see above). The colonies were fed on the host plant on which they were collected. As before, fresh branches of *S.hermannii* or *S.rigescens* were placed, in jars filled with water, in the cages every 2-3 days. Egg cases were removed from the leaves and isolated in hatching trays.

Survival tests were conducted to observe the effects of both host plants on larvae from the two beetle colonies. The tests were conducted in glass cylinders as in the previous experiments (see above). Two hundred first instar hatchlings from each colony were collected; 100 were reared on the field host and the remainder on the other species. Four treatments, comprising larvae of *S.hermannii* and *S.rigescens* origin fed on both *S.hermannii* and *S.rigescens*, were thus tested. Ten larvae were placed in each cylinder, allowing 10 replicates for each treatment. The leaves were kept fresh by placing them on moist cotton wool, which covered much of the lower leaf surfaces and the petioles. Earlier observations revealed that the larvae did not have any preference for the lower leaf surfaces. New leaves were supplied every second day.

The larvae were reared to the adult stage and the mortality and duration of each stage of the life cycle was recorded, as in the previous set of experiments. The mass of the pupae and length of the adults was measured to obtain an assessment of size. Males and females were assessed separately due to the sexual dimorphism for size (see Chapter 7). Kruskal-Wallis tests followed, where appropriate, by Mann-Whitney comparisons were used in the analysis of these data.

Food preference tests were conducted in petri dishes with gauze covered lids, so that the accumulation of possible plant volatiles would not confuse host selection by the beetles. Six leaf discs of 15mm diameter, three from each test plant, were presented to each group of beetles. The discs from the two plants were arranged alternately around the perimeter of the dish. Moist cotton wool on the floor of the dish kept the leaf discs in good condition for the 24 hours duration of the experiments. Twenty five experiments were carried out with beetles of each population, using five beetles per dish. The leaf discs were weighed before the beetles were introduced and again after 24 hours. Control dishes were prepared for each experiment to distinguish between mass reduction due to feeding and to water loss. Wilcoxon signed ranks tests were conducted on the results.

Oviposition preference tests were conducted in gauze-covered cages (20cmx20cmx20cm), to prevent interference from the accumulation of plant volatiles. Two freshly picked leaves from each of the two host plants, each resting on moist cotton in a petri dish, were presented in each cage. The dishes were arranged so that the two leaves from the same host plant were in diagonally opposite corners. Fifteen experiments were carried out with beetles originally collected from each of the two host plants, using a mated pair of beetles in each cage. The experiments lasted for 10 days after deposition of the first egg case. Fresh leaves were supplied daily and the number of egg cases laid on each plant recorded. Wilcoxon signed ranks tests were conducted on the results.

# 3. INSECT HERBIVORE DIVERSITY ON *S.MAURITIANUM* AND THREE OTHER *SOLANUM* SPECIES IN THE EASTERN CAPE

## 3.1. Introduction.

The most common *Solanum* species (excluding the exotic *S.mauritianum*) in the vicinity of Grahamstown are *S.hermannii* and *S.rigescens*. *S.coccineum* is scarce relative to the other species in this area. The distribution, based on currently available records, of these species in South Africa is indicated in Figs. 3.1, 3.2 and 3.3. All three species often occur in the same disturbed habitats as does bugweed. The diversity of phytophagous insect species on bugweed was evaluated and compared with that of the other locally-occurring *Solanum* species. One of these, *S.hermannii*, has added interest in that it apparently also occurs in the mediterranean region, raising the possibility that it may be exotic to southern Africa (Hepper 1978, Wells *et al.* 1986). Goeden (1971a) mentioned the value of using faunistic surveys to determine the indigenous or exotic status of plants. A comparison of the species diversity of phytophagous insects attacking *S.hermannii* and two local species (*S.rigescens* and *S.coccineum*) may provide some insight into the question of whether *S.hermannii* is indigenous.

## 3.2. Insects associated with *S.mauritianum*.

Fourteen regularly-occurring phytophages, together with the unidentified Aphididae, Cicadellidae and Thysanoptera were collected (Table 3.1). On the leaves the more numerous species included an epilachnine ladybird (*Henosepilachna hirta* (Thunberg)), a tip wilter (*Acanthocoris* sp., AcRh 486) and unidentified nymphal aphid and thrip species. *H.hirta* was the only species in this group that inflicted observable damage. The other species occurred in low numbers. Field observations also revealed the occasional presence of various grasshopper species, that seemed to account for much of the limited leaf damage. However, very few were represented in samples since they were easily alarmed and escaped before sampling. Since no clear association was observed

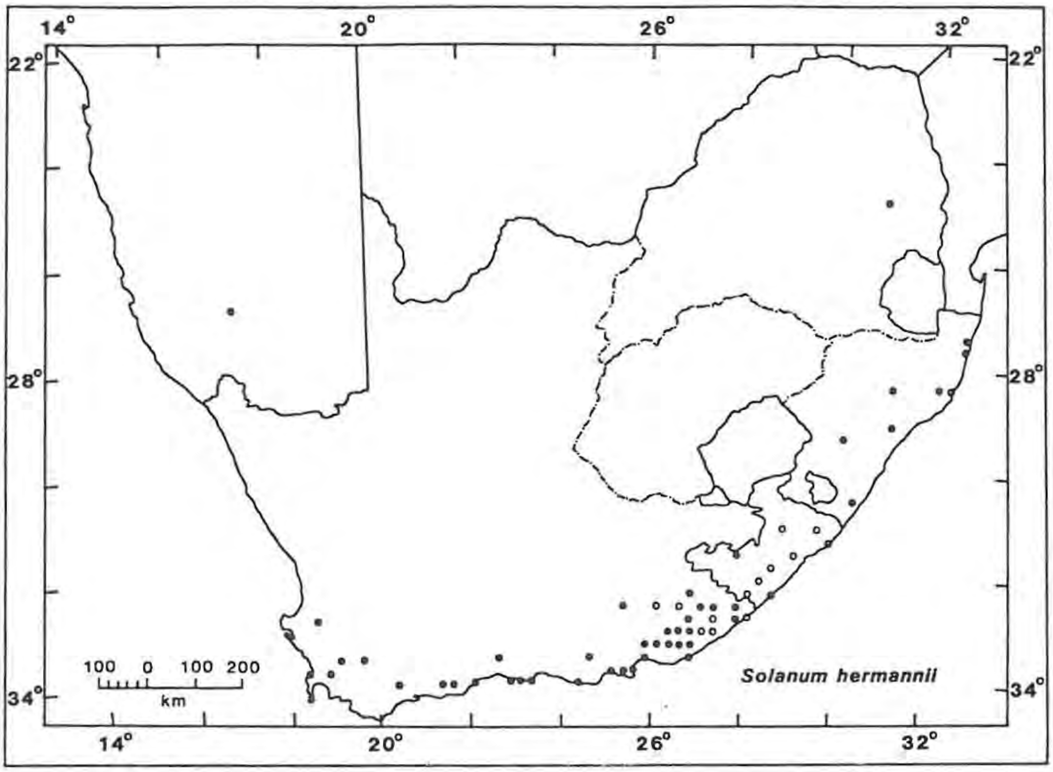

**Fig.3.1.** Distribution of *Solanum hermannii* in South Africa. Closed circles represent records obtained from the Botanical Research Institute in Pretoria and Grahamstown and also specimens collected during the survey and identified by the BRI. Open circles represent records based on own identifications.

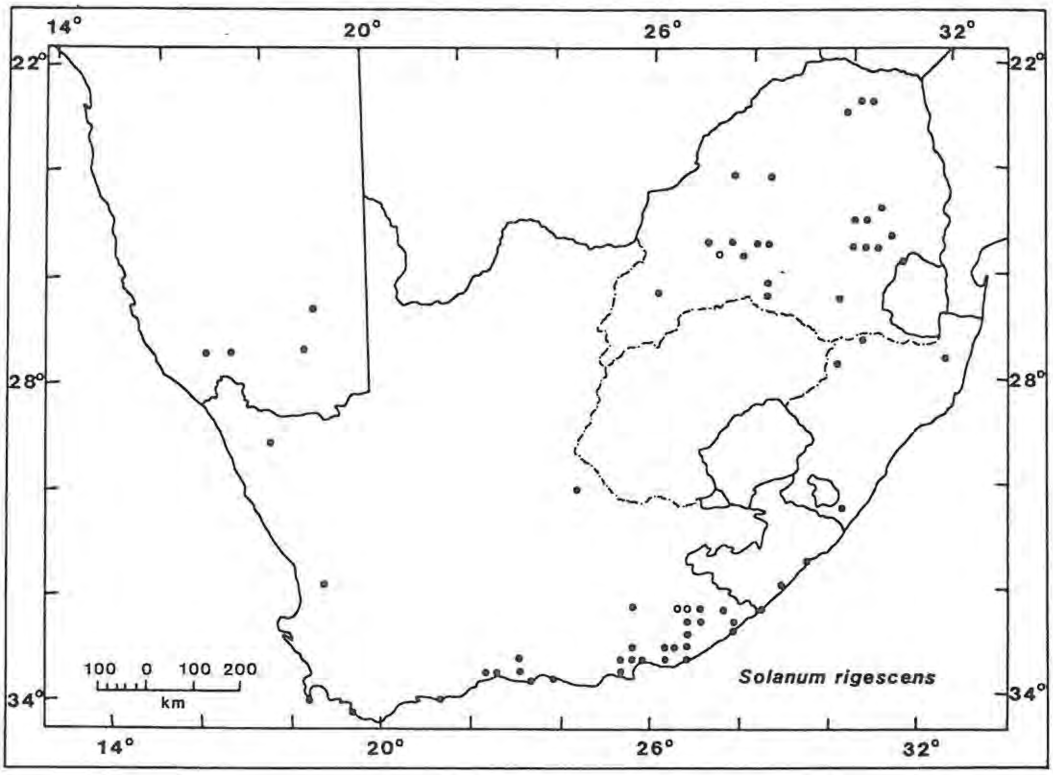

**Fig.3.2.** Distribution of *Solanum rigescens* in South Africa. Closed circles represent records obtained from the Botanical Research Institute in Pretoria and Grahamstown and also specimens collected during the survey and identified by the BRI. Open circles represent records based on own identifications.

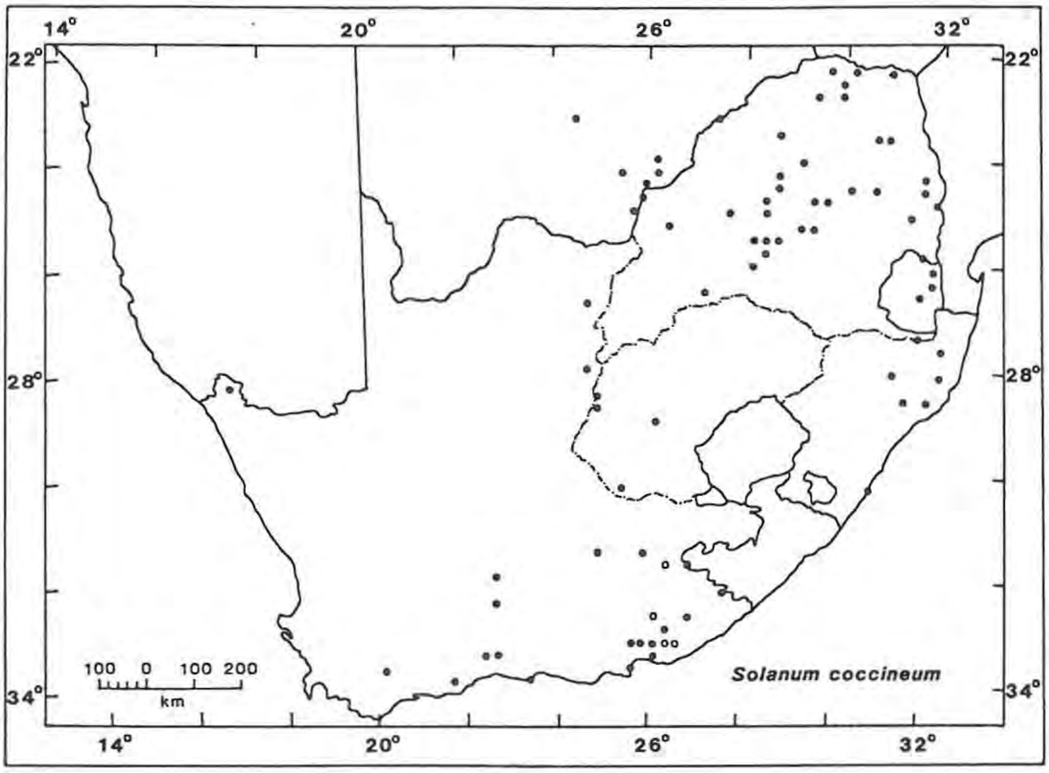

**Fig.3.3.** Distribution of *Solanum coccineum* in South Africa. Closed circles represent records obtained from the Botanical Research Institute in Pretoria and Grahamstown and also specimens collected during the survey and identified by the BRI. Open circles represent records based on own identifications.

with any of the *Solanum* species, grasshoppers are not included in the tables of herbivores.

Table 3.1. Major insect herbivores associated with *Solanum mauritianum* Scop. in the eastern Cape. Species found only once excluded. *

| | *INCIDENCE* ** |
|---|---|
| *LEAVES* | |
| COLEOPTERA | |
| **Chrysomelidae** | |
| *Chaetocnema* sp. (AcRh 465) | 4,6 |
| **Coccinelidae** | |
| *Henosepilachna hirta* (Thunberg) | 16,9 |
| Epilachninae (AcRh 466) | 1,5 |
| **Curculionidae** | |
| *Sibinia* sp. (AcRh 505) | 1,5 |
| **Lathridiidae** | |
| *Corticaria* sp. (AcRh 506) | 1,5 |
| AcRh 549 | 4,6 |
| HEMIPTERA | |
| **Aphididae (various)** | 29,2 |
| **Cicadellidae (various)** | 3,1 |
| **Coreidae** | |
| *Acanthocoris* sp. (AcRh 486) | 10,8 |
| **Lygaeidae** | |
| *Oxycarenus* sp. (AcRh 489) | 3,1 |
| THYSANOPTERA (various) | 10,8 |
| | |
| *FRUIT* | |
| DIPTERA | |
| **Drosophilidae** | |
| AcRh 471 | 6,9 |
| AcRh 472 | 2,8 |
| **Sciaridae (AcRh 469): Natal** | 1,4 |
| **Tephritidae** | |
| *Ceratitis rosa* Karsch | 5,6 |
| LEPIDOPTERA | |
| Unidentified caterpillars (AcRh 568) | 4,2 |
| | |
| *FLOWERS* | |
| COLEOPTERA | |
| **Nitidulidae** | |
| *Pria* sp. (AcRh 504) | 7,8 |
| HEMIPTERA | |
| **Aphididae (various)** | 1,6 |
| THYSANOPTERA (various) | 6,3 |

* Voucher specimens of unidentified species lodged in the Albany Museum (Natural History), Grahamstown, South Africa.

** Percentage of the total number of samples in which the insects occurred.

The stems were almost free from insect attack. A single unidentified fly pupa was, however, found in a stem in December 1985.

Three fly species were reared from fruit in the eastern Cape, the Natal fruit fly (*C.rosa*) and two drosophilids (AcRh 471 and 472). In addition, a sciarid fly (AcRh 469) was reared from fruit collected at Pietermaritzburg, Natal (courtesy of J.H. Hoffmann). Caterpillars of an unidentified moth (AcRh 568) fed externally on the fruit. All of these occurred in a low proportion of the samples. In contrast to local collections, *C.rosa* emerged in large numbers from the samples collected at Pietermaritzburg.

On the flowers, the nitidulid beetle (*Pria* sp., AcRh 504) was the only species that occurred in fair numbers. The adults and larvae of species of *Pria* are known to be pollen feeders (Cooper 1982). However, only adults were collected on the flowers.

## 3.3. Insects associated with *S.rigescens*.

Thirteen regularly-occurring phytophages, together with the unidentified Aphididae and Thysanoptera were collected (Table 3.2). On the leaves, the most common species were the flea beetle (*Chaetocnema* sp., AcRh 465), the tortoise beetle (*C.tigrina*), the epilachnine ladybird (*H.hirta*) and a tip wilter (*Acanthocoris* sp., AcRh 488). The stems were attacked by a gelechiid moth (AcRh 481), whose caterpillars caused large galls on the stems and shoots, and the ripening berries were infested by caterpillars of another gelechiid (*Scrobipalpa* sp., AcRh 572).

The flowers were attacked mainly by a third gelechiid moth (*Scrobipalpa* sp., AcRh 573) and the nitidulid (*Pria* sp., AcRh 504). The gelechiid caterpillars, which resembled those from the berries, consumed the ovaries of the flowers. The adults of the nitidulid beetles fed on pollen and the larvae bored into the stamens. Cecidomyiid larvae (AcRh 578) also bored into the stamens but did not inflict serious damage, probably because of low infestations.

Table 3.2. Major insect herbivores associated with *Solanum rigescens* in the eastern Cape. Species found only once excluded. *

| | *INCIDENCE* ** |
|---|---|
| *LEAVES* | |
| COLEOPTERA | |
| **Chrysomelidae** | |
| *Chaetocnema* sp. (AcRh 465) | 57,7 |
| *Conchyloctenia tigrina* Oliv. | 30,8 |
| **Coccinelidae** | |
| *Henosepilachna hirta* (Thunberg) | 30,8 |
| HEMIPTERA | |
| **Coreidae** | |
| *Acanthocoris* sp. (AcRh 488) | 26,9 |
| **Membracidae (AcRh 485)** | 19,2 |
| **Pentatomidae** | |
| *Dryadocoris apicalis* (H.Sch.) | 19,2 |
| *Nezara viridula* (L.) | 7,7 |
| AcRh 529 | 15,4 |
| *STEMS* | |
| LEPIDOPTERA | |
| **Gelechiidae (AcRh 481)** | 28,6 |
| *FRUIT* | |
| LEPIDOPTERA | |
| **Gelechiidae** | |
| *Scrobipalpa* sp. (AcRh 572) | 44,4 |
| *FLOWERS* | |
| LEPIDOPTERA | |
| **Gelechiidae** | |
| *Scrobipalpa* sp. (AcRh 573) | 65,0 |
| COLEOPTERA | |
| **Nitidulidae** | |
| *Pria* sp. (AcRh 504) | 60,0 |
| DIPTERA | |
| **Cecidomyiidae (AcRh 578)** | 10,0 |
| HEMIPTERA | |
| **Aphididae (various)** | 10,0 |
| THYSANOPTERA (various) | 10,0 |

* Voucher specimens of undetermined species lodged in the Albany Museum (Natural History), Grahamstown, South Africa.
** Percentage of the total number of samples in which the insects occurred.

### 3.4. Insects associated with *S.coccineum*.

Fourteen regularly-occurring phytophages together with the unidentified Cicadellidae were collected (Table 3.3). On the leaves, the flea beetle (*Chaetocnema* sp., AcRh 465), membracids (AcRh 485) and a tip wilter (*Acanthocoris* sp., AcRh 488) were the most numerous. The tortoise beetle (*C.tigrina*) and the epilachnine

Table 3.3. Major insect herbivores associated with *Solanum coccineum* in the eastern Cape. Species found only once excluded. *

| | *INCIDENCE* ** |
|---|---|
| *LEAVES* | |
| COLEOPTERA | |
| **Chrysomelidae** | |
| *Chaetocnema* sp. (AcRh 465) | 44,8 |
| *Conchyloctenia tigrina* Oliv. | 6,9 |
| **Coccinelidae** | |
| *Henosepilachna hirta* (Thunberg) | 3,5 |
| HEMIPTERA | |
| **Cicadellidae (various)** | 6,9 |
| **Coreidae** | |
| *Acanthocoris* sp. (AcRh 488) | 13,8 |
| **Lygaeidae** | |
| *Spilostethus* sp. (AcRh 501) | 10,3 |
| **Membracidae (AcRh 485)** | 17,2 |
| **Pentatomidae** | |
| *Dryadocoris apicalis* (H.Sch.) | 6,9 |
| AcRh 529 | 3,5 |
| **Tingidae** | |
| *Urentius hystricellus* (Richter) | 3,5 |
| LEPIDOPTERA | |
| **Noctuidae** | |
| *Pardasena* sp.nr. *diversipennis* Gaede | 3,5 |
| **Leaf-roller caterpillar (AcRh 512)** | 20,7 |
| *STEMS* | |
| LEPIDOPTERA | |
| **Gelechiidae** (AcRh 480) | 22,7 |
| *FRUIT* | |
| LEPIDOPTERA | |
| **Gelechiidae** | |
| *Scrobipalpa* sp. (AcRh 572) | 28,6 |
| *FLOWERS* | |
| LEPIDOPTERA | |
| **Gelechiidae** | |
| *Scrobipalpa* sp. (AcRh 573) | 25,0 |

* Voucher specimens of undetermined species lodged in the Albany Museum (Natural History), Grahamstown, South Africa.
** Percentage of the total number of samples in which the insects occurred.

ladybird (*H.hirta*), which were numerous on *S.rigescens*, were far less common. Two species of caterpillar were found, one (AcRh 512), pupated in rolled-up leaves, while *Pardasena* sp.nr. *diversipennis* Gaede fed on the leaf surface after nibbling off the trichomes (Hulley 1988). The remaining herbivores occurred only in low numbers.

Caterpillars of the gelechiid moth (AcRh 480), caused large galls on the stems and shoots. The moths appeared to be the same as those on *S.rigescens*, although a different accession number was allocated. The berries, like those of *S.rigescens*, were attacked by the gelechiid moth (*Scrobipalpa* sp., AcRh 572), whose caterpillars infested ripening berries. The flowers were also attacked by the same species of *Scrobipalpa* (AcRh 573, Gelechiidae) as those of *S.rigescens*. The caterpillars similarly fed on the ovaries.

## 3.5. Insects associated with *S.hermannii*.

Twenty eight regularly-occurring phytophages and the unidentified Aphididae, Cicadellidae and Thysanoptera were obtained (Table 3.4). On the leaves, the most important herbivorous species were the flea beetle (*Chaetocnema* sp., AcRh 465), the epilachnine ladybird (*H.hirta*), the tortoise beetle (*C.tigrina*) and a tip wilter (*Acanthocoris* sp., AcRh 487). These species occurred in greater numbers than the other insects and field observations showed that they inflict considerable damage. Although not seen actually feeding, snails were sometimes found at fresh feeding damage and grasshoppers may have been responsible for feeding damage observed in the absence of infestations by the herbivores mentioned above.

The stems were almost free from insect attack. A single fly pupa was, however, found in a stem in December 1985.

The fruit were infested by seven species, of which a pyraustid moth (*Daraba laisalis* (Walker)) was the most prevalent. Caterpillars of the moth infested ripening fruit, causing them to rot. Six fly species also emerged from caterpillar-infested fruit. The most numerous were *Silba ophyroides* (Bezzi) (Lonchaeidae) and an unidentified agromyzid (AcRh 467). Adults and nymphs of the pentatomid, *Dryadocoris apicalis* (H.Sch), were found inside dried-out infested fruit. These probably entered the fruit to attack the seeds, but may also have done so for shelter.

The flowers yielded six phytophagous species. The most prevalent were *Scrobipalpa* sp. nr.*concreta* (Meyrick) (Gelechiidae), cecidomyiids (AcRh 578) and the nitidulid (*Pria* sp., AcRh 504). The gelechiid caterpillars, which caused galling of the flowers, fed on the ovaries. The nitidulid beetles and their larvae, as in *S.rigescens*, fed on pollen and caused some damage to the stamens. Flea beetles (*Chaetocnema* sp., AcRh 465), while causing severe leaf damage, occurred only in low numbers on the flowers.

Table 3.4. Major insect herbivores associated with *Solanum hermannii* in the eastern Cape. Species found only once excluded. *

| | *INCIDENCE* ** |
|---|---|
| *LEAVES* | |
| COLEOPTERA | |
| **Chrysomelidae** | |
| *Conchyloctenia tigrina* Oliv | 26,1 |
| *Chaetocnema* sp. (AcRh 465) | 68,2 |
| Cassidinae (AcRh 569) | 2,3 |
| **Coccinelidae** | |
| *Henosepilachna hirta* (Thunberg) | 40,9 |
| Epilachninae (AcRh 466) | 4,5 |
| Epilachninae (AcRh 543) | 9,1 |
| **Curculionidae** | |
| *Sibinia* sp. (AcRh 505) | 2,3 |
| **Lathridiidae (AcRh 549)** | 3,4 |
| HEMIPTERA | |
| **Aphididae (various)** | 4,5 |
| **Cicadellidae (various)** | 2,3 |
| **Coreidae** | |
| *Acanthocoris* sp. (AcRh 487) | 12,5 |
| **Lygaeidae** | |
| *Spilostethus* sp. (AcRh 501) | 3,4 |
| **Nogodinidae (AcRh 571)** | 3,4 |
| **Membracidae (AcRh 484)** | 7,9 |
| **Pentatomidae** | |
| *Dryadocoris apicalis* (H.Sch.) | 7,9 |
| *Nezara viridula* (L.) | 3,4 |
| AcRh 529 | 1,1 |

| | |
|---|---|
| **Scutelleridae (AcRh 525)** | 5,7 |
| THYSANOPTERA (various) | 3,4 |
| | |
| *FRUIT* | |
| DIPTERA | |
| **Agromyzidae (AcRh 467)** | 24,4 |
| **Drosophilidae** | |
| AcRh 471 | 1,2 |
| AcRh 472 | 1,2 |
| **Lonchaeidae** | |
| *Lamprolonchaeia smaragdi* (Walker) | 1,2 |
| *Silba ophyroides* (Bezzi) | 32,9 |
| **Muscidae** | |
| *Atherigona* sp. (AcRh 470) | 7,3 |
| LEPIDOPTERA | |
| **Pyraustidae** | |
| *Daraba laisalis* (Walker) | 51,2 |
| | |
| *FLOWERS* | |
| COLEOPTERA | |
| **Chrysomelidae** | |
| *Chaetocnema* sp. (AcRh 465) | 11,3 |
| **Nitidulidae** | |
| *Pria* sp. (AcRh 504) | 36,6 |
| DIPTERA | |
| **Cecidomyiidae (AcRh 578)** | 40,8 |
| **Sciaridae (AcRh 577)** | 1,4 |
| HEMIPTERA | |
| **Aphididae (various)** | 4,2 |
| LEPIDOPTERA | |
| **Gelechiidae** | |
| *Scrobipalpa* sp.nr. *concreta* (Meyrick) | 77,5 |

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* Voucher specimens of undetermined specimens lodged in the Albany Museum (Natural History), Grahamstown, South Africa.

** Percentage of the total number of samples in which the insects occurred.

## 3.6. Discussion.

Rather surprisingly, the diversity of phytophagous insects on *S.mauritianum* initially appeared to match the numbers found on indigenous species. A total of 24 species or unidentified higher taxa was collected on *S.mauritianum*, compared to 25 on *S.rigescens* and 21 on *S.coccineum* (see Fig.3.4 which encompasses all herbivores (except grasshoppers), including the rare species). The asymptotes reached by the curves in Fig.3.4, relating cumulative numbers of species to numbers of samples collected, indicated that the great majority of phytophages had been recorded from all of the plants. However, many of these species are polyphagous and feed only

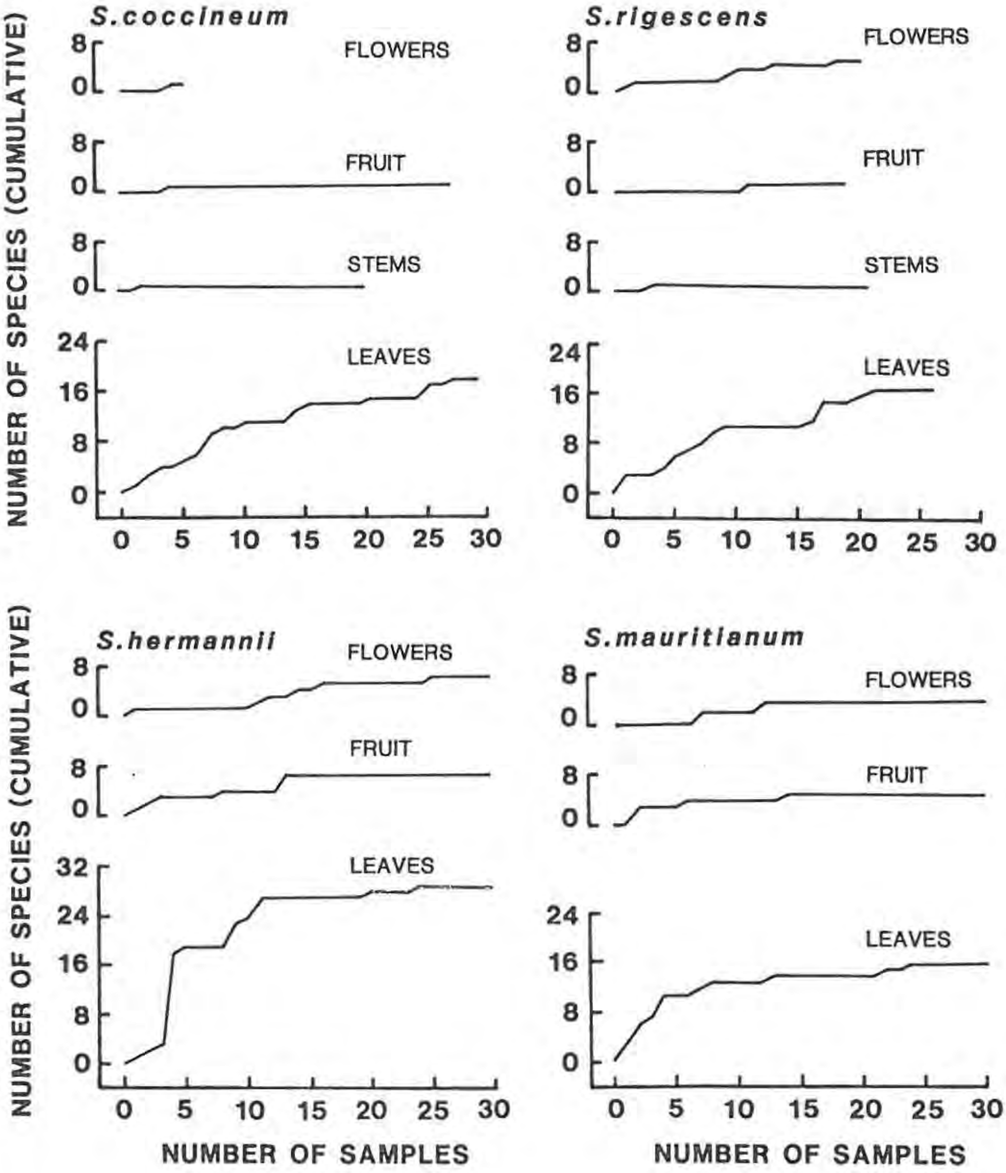

**Fig.3.4.** Numbers (cumulative) of insect herbivore species collected in successive samples of leaves, stems, fruit and flowers of *Solanum coccineum*, *Solanum rigescens*, *Solanum hermannii* and *Solanum mauritianum*. No insects were associated with the stems of *S.hermannii* and *S.mauritianum*.

occasionally on, particularly, *S.mauritianum*. Exotic plants tend to be attacked largely by polyphagous insects (Strong *et al.* 1984).

If one considers only regularly-occurring species (here taken as those occurring in at least 20% of the samples), a different pattern emerges. Only one such species was recorded from *S.mauritianum*, compared to seven on *S.rigescens* and five on *S.coccineum* (Fig.3.5). The single regularly-occurring phytophage on *S.mauritianum* comprised unidentified nymphal aphids. The herbivore community of *S.mauritianum* comprised species that occurred in few of the samples, in contrast to that of *S.rigescens* and *S.coccineum* where more regularly-occurring species dominated (Fig.3.5). *H.hirta*, the only species that inflicted obvious damage on *S.mauritianum*, actually occurred in 17% of the samples collected, and seemed to prefer young to older leaves. There was also a noteworthy lack of insects that regularly affected the fruit and flowers of *S.mauritianum*. This was not the case in *S.rigescens*, *S.coccineum* and *S.hermannii*, where fruit and flowers were regularly attacked. Thus, *S.mauritianum* has a depauperate phytophagous fauna relative to indigenous plants. Field observation showed that this plant is relatively unscathed in comparison to the other species.

The rate at which phytophages colonize introduced plants is affected by at least two factors. These include the range of the introduced plant and the taxonomic, phenological, biochemical and morphological match between the introduced plant and native plants (Strong *et al.* 1984). These authors also suggest that while the insects that colonize introduced plants are usually broadly polyphagous species, some oligophagous species from taxonomically or biochemically related plants may also do so. Of the 19 major species found on *S.mauritianum* (Table 3.4), 13 also occurred on *S.hermannii* and six and four on *S.rigescens* and *S.coccineum* respectively. The species shared by *S.mauritianum* with *S.rigescens* and *S.coccineum* all occurred on *S.hermannii*. The "pool" of *S.mauritianum* colonists, around Grahamstown, thus originates mainly from the phytophagous fauna of *S.hermannii*. This could imply a closer match between

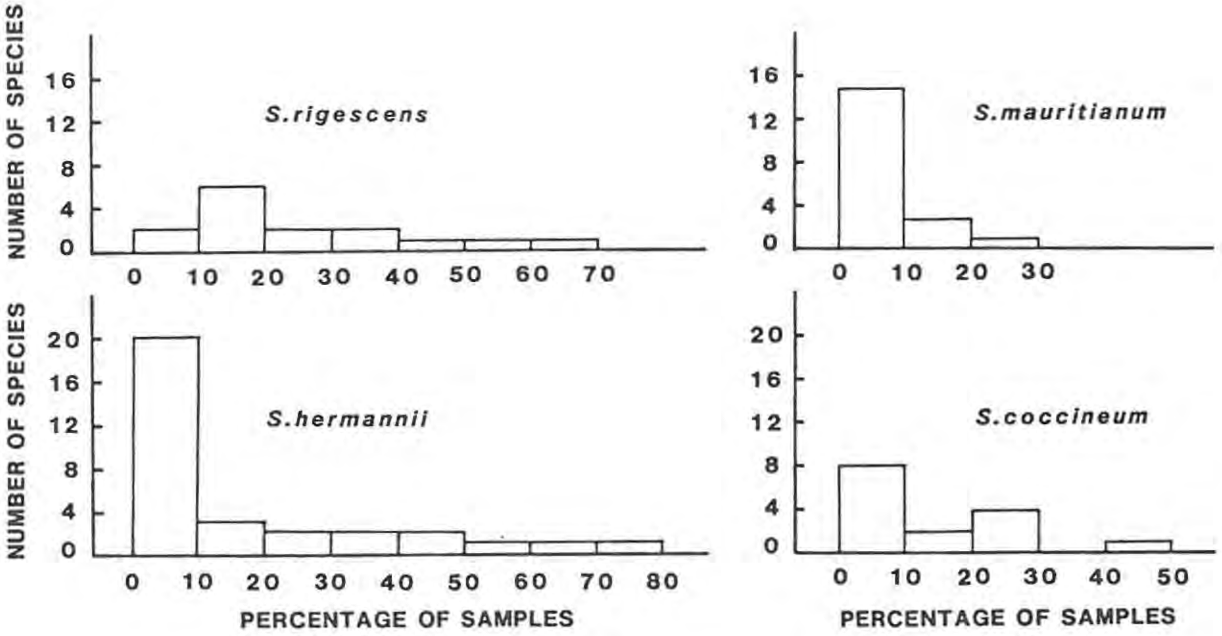

**Fig.3.5.** The representation of insect herbivore species in samples taken from each of four *Solanum* species. Each bar in the histogram represents that group of insect species which was found in a particular percentage class of the total number of samples of the plant species. For example, in *Solanum hermannii*, 20 species occurred in under 10% of samples, and 3 in more than 9% but less than 20%. Common species are designated as those found in at least 20% of samples.

*S.hermannii* and *S.mauritianum*, than the other two species. It could also be explained by *S.hermannii* and *S.mauritianum* often growing together in the same habitat, and *S.hermannii* being the most commonly occurring species of the three.

Of the phytophages collected from *S.mauritianum* in the eastern Cape (excluding the polyphagous acridids mentioned), only the epilachnine ladybird (*H.hirta*) has shown the ability to inflict noticeable damage. This damage, however, was less than that observed on the three native hosts. It may be that *S.mauritianum* is a "difficult" food plant relative to the local *Solanum* species. An alternative explanation is that phytophages do not readily adapt to new hosts, and that unless the new host fortuitously has appropriate chemical or other characteristics that preadapt the phytophages to use it, colonization will be low. Two possible barriers to insect herbivory on bugweed are the dense trichomes and secondary chemicals (Levin 1973). When leaves of various *Solanum* species are examined under the microscope, it can be seen that *S.mauritianum* has a high density of leaf trichomes relative to most of the local *Solanum* species. Young leaves of *S.mauritianum* bear fewer trichomes, and emit more weakly the characteristic odour, than normal leaves when crushed. This suggests a lower concentration of at least one secondary chemical. The observation that the ladybird *H.hirta* appears to prefer less trichomate leaves may thus have a chemical as well as a physical basis.

Although *S.hermannii* is regarded as indigenous to South Africa (Martin and Noel 1960, Gibbs Russell *et al.* 1987), Hepper (1978) stated that it could be a very early introduction from southern Europe to the Cape or vice versa. A direct comparison of insect diversity on the plant in the two regions would be useful in helping to decide where the plant originated, but it has not been possible to obtain comparative data on European *S.hermannii*. However, the phytophagous fauna of *S.hermannii* has been compared with that of *S.coccineum* and *S.rigescens*, which are regarded as indigenous (Wells *et al.* 1986, Gibbs Russell *et al.* 1987). Although 42 species were found on *S.hermannii*, only 21 and 25 species were collected on *S.coccineum* and *S.rigescens* respectively (Fig.3.4). Of the herbivore species that occurred in at least 20% of the samples collected, nine were collected on *S.hermannii*, compared to seven and five species on *S.rigescens* and *S.coccineum* respectively (Fig.3.5). There is thus no reason on these grounds to assume that *S.hermannii* is not indigenous, since its herbivore community is more closely matched to that of *S.rigescens* than to *S.mauritianum* (Fig.3.5). The poorer species diversity on *S.coccineum* is probably influenced by the effect of local abundance (see Strong *et al.* 1984), since it is scarce where much of this survey was actually conducted (Grahamstown).

Although the phytophagous fauna of *S.hermannii* is diverse relative to the other *Solanum* species examined, it appears depauperate when compared to that of *S.elaeagnifolium*, in its native southern U.S.A. Goeden (1971a) collected 123 phytophagous species on this plant and although it was sampled over a much wider geographical range the duration of the survey was limited to irregular intervals in one summer only. It seems unlikely that the list of herbivores from *S.hermannii* can be drastically extended by increasing the geographical range of the surveys in South Africa. A number of hypotheses have been advanced to account for differences in the numbers of insect herbivores associated with different plant species. These are summarized by Strong *et al.* (1984). Several of these could explain the species diversity difference between *S.hermannii* and *S.elaeagnifolium* and this question cannot be persued any further on present knowledge.

Only nine of the 32 major species on *S.hermannii* were common on the plant and only five of these inflicted appreciable damage. Although it is difficult to evaluate the ultimate effect of herbivore damage on a plant (Crawley 1987), this suggests that insect attack may not be the only factor influencing the distribution and numbers of *S.hermannii*. Other factors which may influence the distribution of *S.hermannii*, include climatic and soil conditions as well as interspecific competition from other plants. Interspecific competition may be important, since *S.hermannii* appears to be confined to disturbed areas, where one would expect reduced competition. *S.hermannii* occupies similar habitats in Australia (Symon 1981). The distribution of *S.hermannii* appears to be patchy, which could be due to the patchiness of its habitat but may relate to its means of dispersal. Although both *S.hermannii* and *S.mauritianum* can reproduce by seeds, a major difference is that *S.mauritianum* fruits are eaten by a number of bird species. These include Rameron Pigeons, Speckled Mousebirds, Blackeyed Bulbuls and Blackcollared Barbets. Birds were never observed eating *S.hermannii* fruit, and it is unclear at present how their seeds are dispersed, although small mammals are a possibility.

The phytophagous fauna of *S.mauritianum* in South America is much richer than it is in the eastern Cape. A survey by Neser (1984, 1986) in South America indicated a wide range of natural enemies, suggesting that insect herbivory may be important as a controlling factor there. Natural enemies imported from South America, could occupy many of the vacant niches which characterize bugweed in South Africa. Since bugweed is spread by means of seeds, and fruit and flowers seem to be relatively unscathed locally, natural enemies which attack reproductive tissues should be strong candidates for introduction. However, stem and leaf associated species are required to reduce existing infestations, since very few leaf feeders and no stem borers were recorded. The scope for biological control thus appears to be promising.

# 4. SEASONAL ABUNDANCE OF COMMON *SOLANUM* HERBIVORES

## 4.1. Introduction.

The insect herbivore communities of the exotic *S.mauritianum* and some indigenous *Solanum* species in the eastern Cape were described and compared (Chapter 3). The more common herbivores included a number of oligophagous species, some of which caused a high incidence of damage. Studies on the biology and seasonality of these species can be of importance in evaluations of natural and biological control.

In order to investigate the seasonal occurrence of these herbivores on *S.mauritianum*, samples were taken on three occasions over a period of a year. For comparison, samples were also taken from *S.hermannii*, the only other species of *Solanum* sufficiently abundant in the area for this purpose.

*S.hermannii* (bitter apple, sodom apple) is common in disturbed areas and is regarded as a minor weed (Wells *et al*. 1986). It has been declared a noxious weed in some states in Australia, but rarely assumes serious proportions (Symon 1981).

## 4.2. Biology and seasonal abundance of some common herbivores.

a. *Chaetocnema* sp. (AcRh 465) (Chrysomelidae: Alticinae)

Flea beetles were the most numerous insects on the leaves of *S.hermannii* (Fig.4.1). They were also numerous on *S.rigescens* and *S.coccineum* (Chapter 3). These beetles appeared to represent only one species, but, since specific identifications have not been obtained, this is not certain. Occasional individuals were also found on *S.mauritianum*, although densities were negligible in comparison with *S.hermannii*. Adult feeding caused characteristic holes in the leaves, which in heavily infested leaves produced a "shot hole" effect. The beetles were also found feeding on the flowers of *S.hermannii*. The beetles presumably oviposited in the

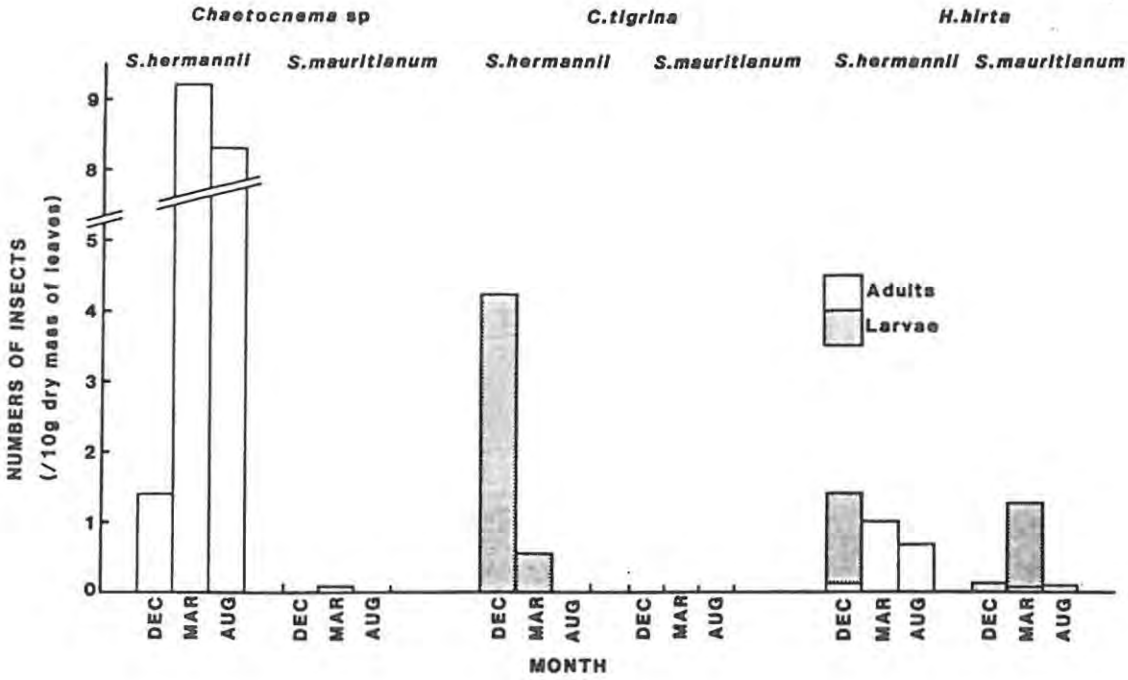

**Fig.4.1.** Seasonal abundance of three major folivores, *Chaetocnema* sp., *Conchyloctenia tigrina* and *Henosepilachna hirta*, on *Solanum hermannii* and *Solanum mauritianum*.

soil at the base of the plants, as flea beetle larvae are generally soil-inhabiting (Endrödy-Younga 1985).

The density of the beetles on *S.hermannii* varied seasonally during the study period (Fig.4.1). Numbers were low in December, and high in March and August. The flea beetles were unusual in their continuing high density on *S.hermannii* during winter. The densities on the plants of all other species dropped at this time.

b. *Conchyloctenia tigrina* Oliv. (Chrysomelidae: Cassidinae)

Tortoise beetles were the second most common species on the leaves of *S.hermannii* (Fig.4.1). They were also numerous on *S.rigescens*, but rare on *S.coccineum* (Chapter 3). Tortoise beetles were never found on bugweed. Feeding by both adults and larvae caused considerable damage to the leaves of *S.hermannii*, which were skeletonized at high population densities. An interesting behavioural aspect of their feeding was their ability to bite off the leaf trichomes, thus "shaving" parts of the leaf before they fed. This behaviour was also suggested in the Argentine tortoise beetle, *G.lutescens*, which was evaluated as a biological control agent for the exotic *S.elaeagnifolium* (Siebert 1975).

The beetles oviposited on the undersurfaces of the leaves. The eggs were heavily parasitized by a species of *Tetrastichus* (Eulophidae). A chalcidid (AcRh 518) was reared in high numbers from field-collected pupae and may have parasitized either the late instar larvae or the pupae.

Larval numbers on *S.hermannii* were highest during December, declined by March and none was found in August (Fig.4.1). No adults appeared in the samples, although beetles were found on *S.hermannii* at other sites.

c. *Henosepilachna hirta* (Thunberg) (Coccinelidae: Epilachninae)

Herbivorous ladybirds were the third most common species on the leaves of *S.hermannii*, where they caused considerable damage (Fig.4.1). They were also numerous on *S.rigescens* but rarer on *S.coccineum* leaves (Chapter 3). Adult and larval feeding scars of *H.hirta* were characterised by track-like patterns on the leaves, which after some days resulted in large holes. *H.hirta* was the only species which caused obvious damage to the leaves of *S.mauritianum*, and was also collected from *Solanum aculeatissimum* Jacq. and *Solanum gracile* Dun. The reported status of *H.hirta* as a pest of potato crops (Jack 1913, Annecke and Moran 1982) and vegetable gardens (Ballard 1914) is indicative of its wide host range. In the laboratory it fed readily on the exotic weed *S.elaeagnifolium* (satansbos). On *S.mauritianum*, young or regrowth leaves appeared to be more susceptible to ladybird damage. This is probably related to the observation that these leaves had fewer trichomes and possibly lower levels of secondary compounds than older leaves (Chapter 3).

The seasonal occurrence of adults and larvae of *H.hirta* on both *S.hermannii* and *S.mauritianum* is shown in Fig.4.1. On *S.hermannii*, larval numbers were high during December, while none was collected during March and August. Adult numbers were low in December and higher during March and August. On *S.mauritianum*, larval numbers were low during December, considerably higher during March and zero by August. Adult numbers were zero in December and low during March and August. Numbers of adults and larvae were always higher on *S.hermannii*, except during March when a far greater number of larvae was found on bugweed. This value should, however, be treated with caution, since it was due to large numbers of first instar larvae collected on only two plants of the twenty sampled.

### d. *Acanthocoris* cf. *fasciculatus* F. (Coreidae)

What appeared to be a single species of tip wilter, *A.* cf. *fasciculatus*, occurred on *S.hermannii*, *S.mauritianum* and *S.rigescens* (AcRh 486). The same species (AcRh 553) was also found on *S.aculeastrum* Dun. and *S.incanum* in Zimbabwe and on *S.panduriforme* in Zululand. Another species of *Acanthocoris* occurred on *S.hermannii* (AcRh 487) and a third on *S.coccineum* (AcRh 488). *Acanthocoris fasciculatus* F. was recorded on *S.mauritianum* and other solanaceous plants (Roberts 1930). Adults and nymphs often formed dense aggregations on the stems and tips of the shoots. The eggs were laid in batches on the undersurfaces of the leaves. Scelionid parasitoids (AcRh 607) were reared from eggs collected on *S.mauritianum*.

Although southern African tip wilters are known to cause wilting and die-back of the shoots of some plants (Jacobs 1985), the actual amount of damage due to *Acanthocoris* sp. was not determined. No severe wilting was, however, observed, even in shoots with large numbers of insects feeding on them. Tip wilters were only recorded during December on *S.mauritianum* and during March on *S.hermannii*. Occurrence seems to be localised and sporadic, judging by incidence observed in other samples.

### e. *Daraba laisalis* (Walker) (Pyraustidae)

The caterpillars of this moth fed in the fruit of *S.hermannii*. They appeared to infest only maturing fruit, since no caterpillars were found in fruit still with immature seeds. Mature fruit, only, were thus chosen when seasonal infestation rates were compared. The caterpillars ate the fruit contents, including some of the seeds, causing the fruit to rot. This encouraged secondary infestation by flies (see below). Pupation probably occurred on the ground, since no cocoons were observed on plants in the field. The moths have a wide host range within the genera *Solanum* and *Lycopersicum* (Pinhey 1975), although they have not been recorded as pests of either potatoes or tomatoes (see Annecke and Moran 1982). The moths were also reared from indigenous solanums, that have large yellow fruit similar to those of *S.hermannii*. These include *S.aculeatissimum*, *S.panduriforme* and *S.incanum*. The latter two species were sampled in Natal and Zimbabwe, respectively.

The infestation in *S.hermannii* fruit appeared to be seasonal (Fig.4.2). The percentage of mature infested fruit was highest during March and far lower during December and August (Fig.4.2b). However, due possibly to a shortage of suitable mature fruits, caterpillar numbers per 10g dry mass of infested fruit was higher in December than in March (Fig.4.2a).

Two braconid parasitoids, *Bracon* sp. (AcRh 476) and *Chelonus* sp. (AcRh 498), emerged from earlier samples of fruit. It seems likely that they, like most members of the group (Prinsloo and Eardley 1985), attack caterpillars. These parasitoids were not found in the seasonal study samples.

Three fly species, *S.ophyroides* (Lonchaeidae), *Atherigona* sp. (Muscidae) and an agromyzid (AcRh 467), were associated with caterpillar-damaged *S.hermannii* fruit. These appeared to be secondary invaders, since they were found only in fruit in an advanced state of decay, associated with the presence of caterpillars. In addition, recently attacked fruit, containing only small caterpillars, yielded no flies. However, *S.ophyroides* was reported as a primary attacker of *S.hermannii* fruit (Munro 1923 in McAlpine 1960).

The frequency of occurrence of the three flies appeared to be seasonal. Infestation of caterpillar-infested fruit by fly larvae was high in December and March, but fly larvae were absent in August (Fig.4.2a). Counts of adult flies from emergence boxes provided seasonal data on the individual fly species (Fig.4.3). The agromyzid was the most numerous, with very high numbers during December and March. Numbers of *S.ophyroides* were relatively low during December, but were much higher during March. *Atherigona* sp. was rare, and was only reared in very low numbers during March. None of the flies was reared during August confirming the result shown in Fig.4.2a, although caterpillar-infested fruits were present at this time. The damage caused by the flies to the host plant was difficult to distinguish from that caused by the *D.laisalis* caterpillars which always occured with them in the fruit.

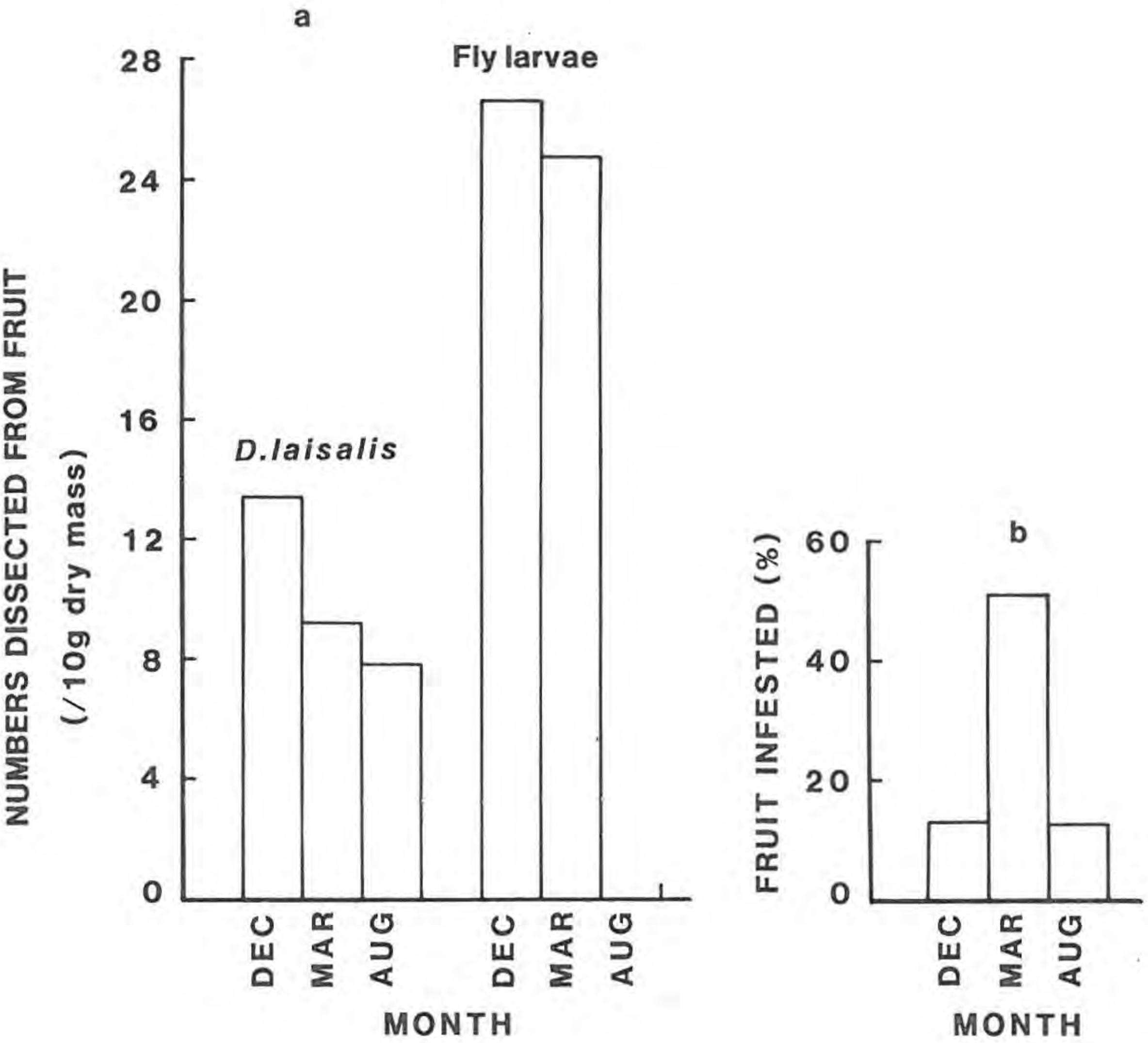

Fig.4.2. Infestation of *Solanum hermannii* fruit by *Daraba laisalis* caterpillars and dipteran larvae (dissected from fruit). a. Seasonal infestation rate in infested fruit. b. Seasonal percentages of mature fruit infested by *D.laisalis*.

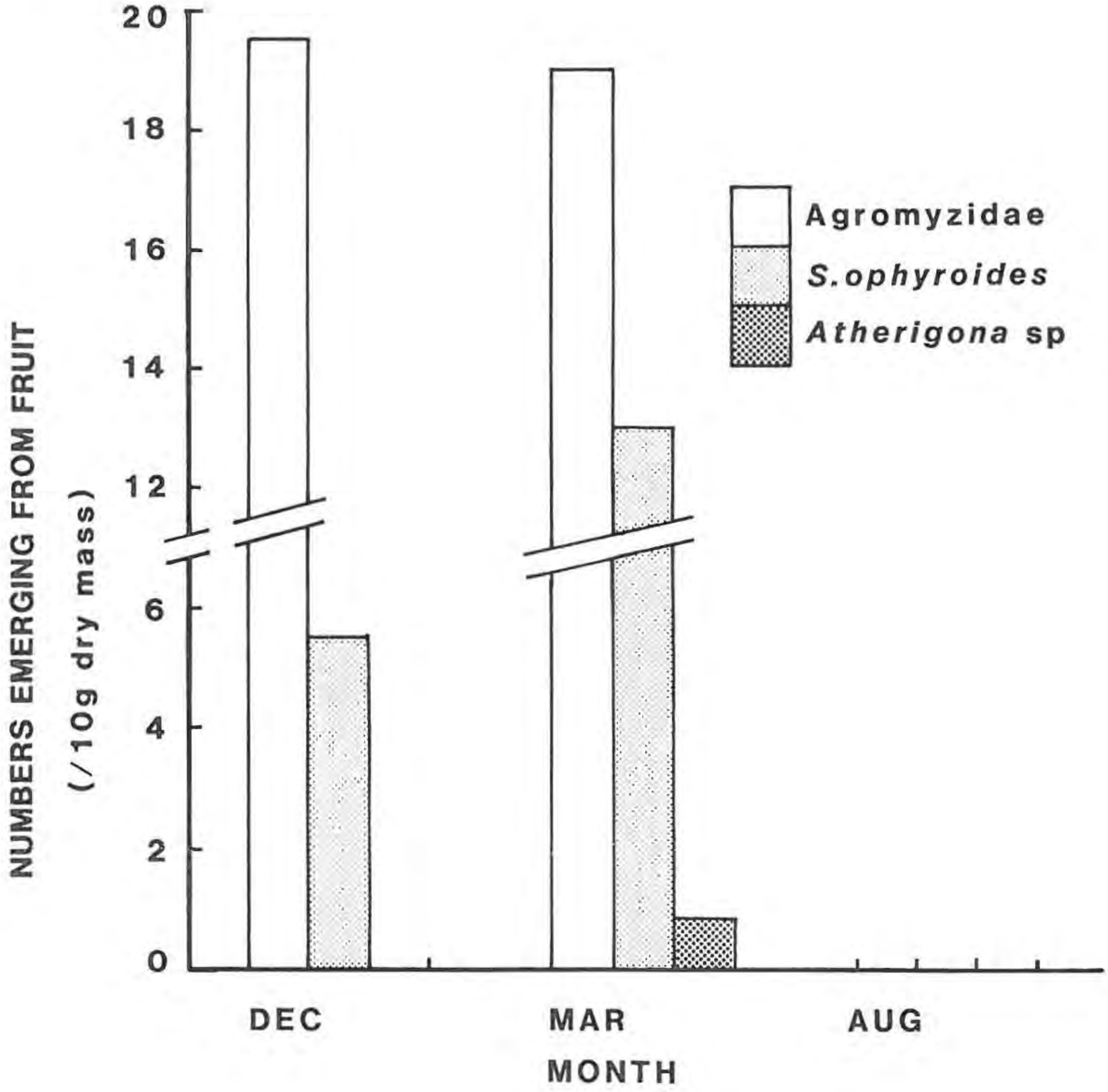

Fig.4.3. Seasonal incidence of three fly species in *Solanum hermannii* fruit (adults from emergence cages).

f.*Scrobipalpa* sp.nr.*concreta* (Meyrick) (Gelechiidae)

Caterpillars of this moth (AcRh 479) caused galling of the flowers of *S.hermannii*. The galled flowers became abnormally large and the petals did not separate, maintaining a budlike condition. The caterpillars occurred singly and destroyed the ovary during feeding. Developing caterpillars changed colour from dull translucent white to a bright pink, with two to four white transverse bands on the anterior region. This may be an aposematic phase, since the caterpillars leave the galls to pupate. Pupation probably occurred off the plant, since no pupae were found on plants in the field.

Similar caterpillars (AcRh 573) fed on the ovaries of flowers of *S.rigescens* and *S.coccineum* (Chapter 3), although these flowers did not develop the galled appearance. These moths were similar to *S.* sp. nr. *concreta* and to each other, although they may not all represent the same species. No caterpillars were encountered on the flowers of *S.mauritianum*. Similar moths (AcRh 572) were also reared from berries of *S.coccineum* and *S.rigescens* (Chapter 3). It is possible that the moths oviposit on berries when flowers are not available, or vice versa. A seasonal change in behaviour was recorded in another gelechiid, *Frumenta nundinella* (Zeller), which attacked *Solanum carolinense* L. in the U.S.A. (Bailey and Kok 1982). In this species, first generation caterpillars fed on the terminal growth parts while second generation caterpillars attacked fruit.

The frequency of *S.* sp.nr. *concreta* on *S.hermannii* appeared to vary seasonally (Fig.4.4). Numbers were high during December, but higher in March and lower in August. The seasonal variation is apparently not due to the availability of flowers since many unaffected flowers were available in all seasons (Fig.4.5b).

The caterpillars infesting flowers of *S.hermannii* were parasitized by two braconids (*Apanteles* sp.(AcRh 477) and *Bracon* sp. (AcRh 510)). The number of both parasitoids was high in relation to the number of moths reared (Fig.4.5a). The same braconid species were reared from flowers of *S.rigescens*, supporting the suggestion

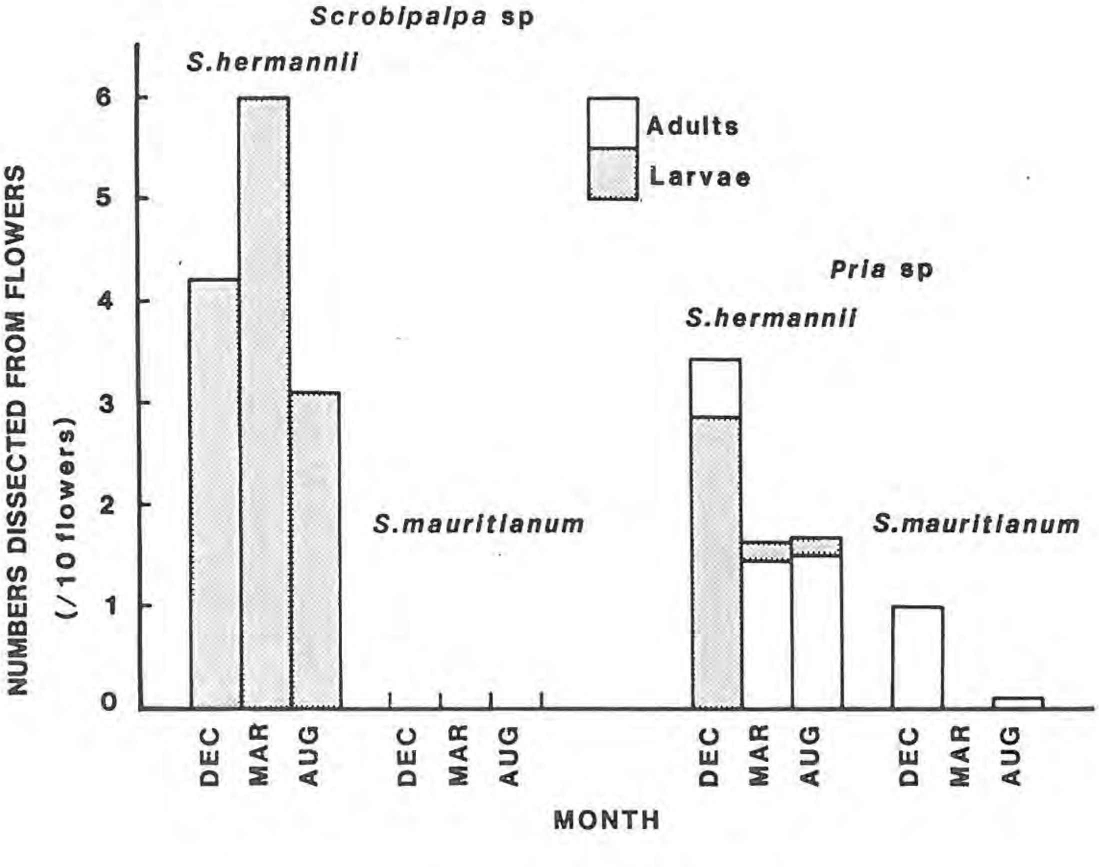

**Fig.4.4.** Seasonal incidence of two major herbivores dissected from flowers of *Solanum hermannii* and *Solanum mauritianum*.

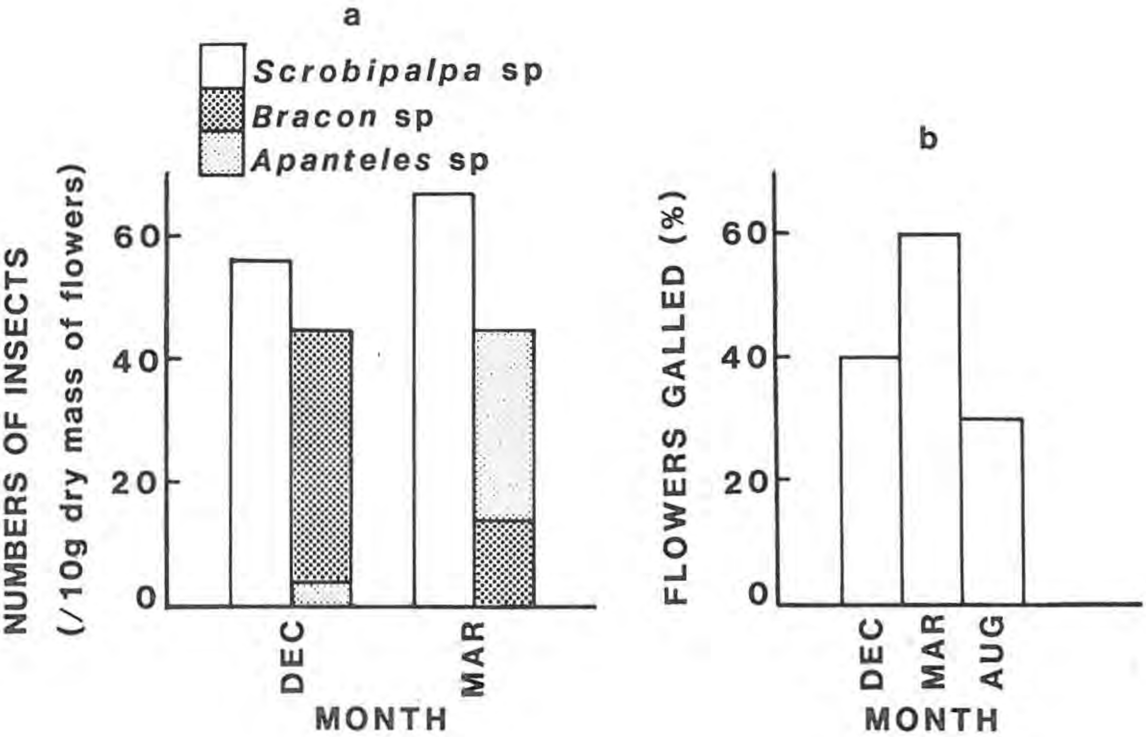

**Fig.4.5.** Galling of *Solanum hermannii* flowers by caterpillars of *Scrobipalpa* sp.nr. *concreta*. a. Seasonal incidence of moths and two parasitoid species (adults emerging from flower galls). Moths and parasitoids were absent from the August sample. b. Seasonal incidence of galled flowers.

that the same species of caterpillar attacks the flowers of both plants.

Turning to the fruit-infesting caterpillars of *S.coccineum* and *S.rigescens*, caterpillars from *S.coccineum* harboured a eurytomid (*Eurytoma* sp. (AcRh 475)) in addition to an *Apanteles* sp. (AcRh 497) apparently identical to that in the flowers of *S.hermannii* and *S.rigescens*. Those of *S.rigescens* were attacked by a different braconid (AcRh 515) in addition to the same *Eurytoma* sp. Different parasitoid species reared from fruit and flowers may suggest different host species.

g. *Pria* sp. (AcRh 504) (Nitidulidae)

*Pria* comprises 17 southern African species (Cooper 1982). Their life history is largely unknown, except for the observation that they are pollen feeders as adults and larvae (Skaife 1979; Endrödy-Younga 1985). Only minor studies of the life history of *Pria dulcamarae* (Scopoli), which attacks *Solanum dulcamara* L. and *Solanum nigrum* L. in Europe, have been made (see Cooper 1982). Eggs, larvae and adults were collected from *S.hermannii* while only adults were collected from *S.mauritianum*. Eggs were laid amongst the stamens, and larvae were observed to have bored into the anthers. No pupae were found on the plants. The larvae may pupate in the soil, like those of *P.dulcamarae* (Cooper 1982). Cooper also mentioned that although the adults often attacked a wide variety of hosts, this polyphagy did not necessarily occur in the larvae. This may explain why no larvae were collected from *S.mauritianum*. The effect on host plant fitness of pollen feeding by *Pria* sp. is difficult to assess, since pollen is normally produced in excess.

The frequency of larvae and adults on *S.hermannii* and adults on *S.mauritianum* varied seasonally (Fig.4.4). On *S.hermannii*, the greatest numbers of adults and larvae were recorded in December. In December, numbers of adults on *S.mauritianum* were considerably lower than those on *S.hermannii*, and were negligible in March and August.

## 4.3. Discussion.

Five of the common phytophages discussed caused significant damage to *S.hermannii*. These were the flea beetle (*Chaetocnema* sp.), the tortoise beetle (*C.tigrina*) and the epilachnine ladybird (*H.hirta*) which all attacked foliage, the fruit-boring moth (*D.laisalis*) and the flower-galling moth (*S.* sp.nr.*concreta*). Only *H.hirta* was observed to damage *S.mauritianum* and only to a limited extent. The amount and nature of the damage caused by the tip wilters (*A.* cf. *fasciculatus*), the three saprophagous fly species and the nitidulid (*Pria* sp.) was not as obvious.

The damage inflicted by the five important species varied seasonally. During the early growing season, the leaves of *S.hermannii* were attacked mainly by tortoise beetles and to a lesser degree by flea beetles and ladybirds. Towards the end of the growing season, most of the damage to the leaves was due to flea beetles and to a lesser degree to ladybirds and tortoise beetles. This situation was maintained during winter, except that tortoise beetles did not occur on the plants. The foliage of *S.hermannii* was thus strongly attacked over all three seasons sampled. However, although particular plants were sometimes defoliated, the damage never reached such proportions that a food shortage for herbivores might have resulted. Many undamaged or lightly damaged plants could always be found nearby.

The reproductive tissues of *S.hermannii* were not strongly affected in all of the three seasons sampled. The percentage of mature fruit infested by caterpillars of *D.laisalis* was only 12% during the early growing season, reached a peak of 50% at the end of the growing season and declined again to 12% during winter (Fig.4.2b). Similarly the percentage of flowers galled by caterpillars of *S.* sp.nr. *concreta* was 40 % during the early growing season, reached a peak of 60% at the end of the growing season and declined again to 30% during winter (Fig.4.5b). Parasitism of the gall caterpillars by the two braconids was also seasonal. Both parasitoids were solitary. *Bracon* sp. accounted for 92 % of the parasitism in the early growing season, while *Apanteles* sp. accounted for 71 % at the end of the growing season (Fig.4.5a). Parasitoids were not found in the winter sample. These parasitoids did not, however, directly reduce flower damage, since the caterpillars had already eaten the ovaries by the time they died. The parasitoids presumably do have an indirect impact by reducing population levels of the moth.

Harris (1973) devised a scoring system whereby the relative effectiveness of herbivorous insects for biological weed control could be determined. Insects are rated according to 12 criteria which included host specificity, nature of feeding damage, feeding behaviour and phenology of attack. Using this system, the five species most damaging to *S.hermannii* were rated as follows: 1) *D.laisalis*, 2) *C.tigrina*, *H.hirta* and *S.* sp.nr.*concreta* and 3) *Chaetocnema* sp. The potential of these insects as biological control agents in countries where *S.hermannii* has become a problem further depends upon screening tests and life history studies. The value of oligophagous agents such as these would depend on the limits of their host range and whether this included plants of economic importance. The epilachnine ladybird (*H.hirta*) could thus be immediately excluded from further studies since it is a minor pest of potatoes.

# 5. FURTHER SURVEYS OF *S.MAURITIANUM* AND SOME INDIGENOUS *SOLANUM* SPECIES IN NATAL AND THE TRANSVAAL

## 5.1. Introduction.

Surveys of the exotic weed *S.mauritianum* in the eastern Cape (Chapter 3) revealed an impoverished herbivore fauna and consequently a low incidence of damage relative to indigenous species of *Solanum*. The most common insects of *Solanum* plants in the eastern Cape comprised a group of oligophagous species, very few of which fed on *S.mauritianum* (Chapter 4). Further faunistic surveys of *S.mauritianum* were carried out in Natal-Zululand and the Transvaal, where the plants are also widespread. The eastern Cape may be near the edge of the range of *S.mauritianum*. These surveys were conducted to check the possibility that, for this reason, *S.mauritianum* may have fewer herbivores in the area relative to other parts of South Africa.

The survey also served to obtain information on indigenous species of *Solanum* not normally encountered in the eastern Cape. The most abundant of these were *S.panduriforme* and *S.incanum*. The distributions of these species in South Africa are indicated in Figs. 5.1 and 5.2. Whereas *S.hermannii* appeared to dominate the eastern Cape *Solanum* flora (Chapter 3), it seemed to be replaced by *S.panduriforme* in other areas, particularly the Transvaal. *S.panduriforme* and *S.incanum* were also sampled opportunistically in Zimbabwe. The herbivore faunas of these two species were compared with those of indigenous *Solanum* species of the eastern Cape.

Of the commonly-occurring *Solanum* species in the eastern Cape, only *S.hermanni* was encountered in the survey. The distribution of this species seems to encompass mainly the coastal regions of the Cape Province (Fig.3.1), with a limited presence in Natal. Although further collections were limited by the relative scarcity of this species in the areas sampled, the list of insect herbivores was extended and compared to that of the eastern Cape.

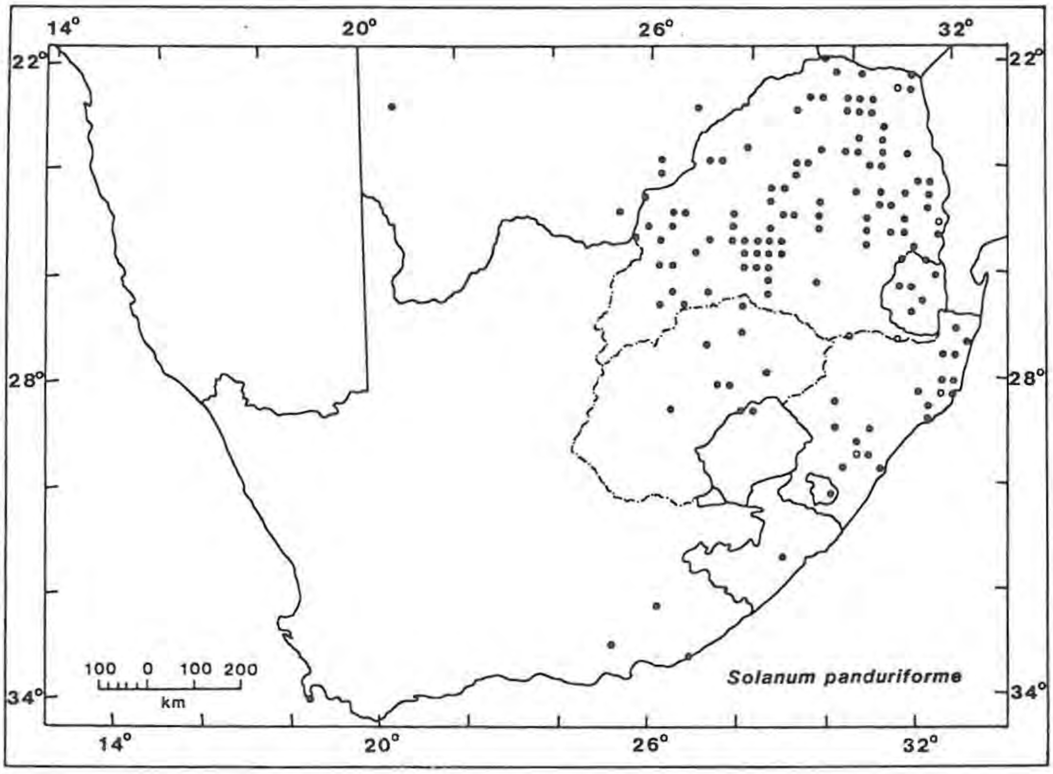

**Fig.5.1.** Distribution of *Solanum panduriforme* in South Africa. Closed circles represent records obtained from the Botanical Research Institute in Pretoria and Grahamstown and also specimens collected during the survey and identified by the BRI. Open circles represent records based on own identifications.

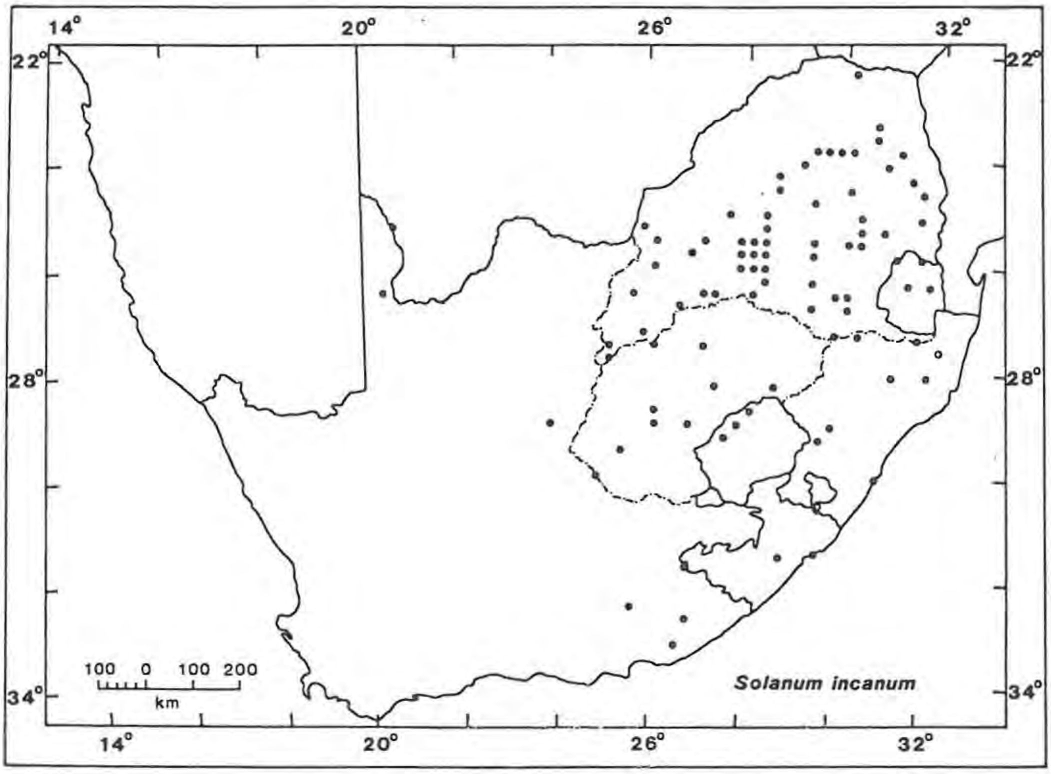

**Fig.5.2.** Distribution of *Solanum incanum* in South Africa. Closed circles represent records obtained from the Botanical Research Institute in Pretoria and Grahamstown and also specimens collected during the survey and identified by the BRI. Open circles represent records based on own identifications.

## 5.2. Status of *S.mauritianum*.

The Natal-Zululand survey indicated that *S.mauritianum* was very common around Weza to the extent where it was regarded as a serious problem in the timber plantations (Fig.1.2). The plants in this region were in good condition and showed very little signs of insect damage. The same was true of an area near Port Shepstone, where, however, the variety of generalist insects such as grasshoppers and scarabaeoid beetles was greater. While no insects were reared from fruit collected at Weza, large numbers of Natal fruit fly (*C.rosa*) emerged from Port Shepstone fruit. Fruit flies were also reared in high numbers from fruit collected earlier at Pietermaritzburg, but were rarely reared from eastern Cape fruit (Chapter 3). However, it appeared that the apparent greater species diversity of Natal *S.mauritianum* was simply a reflection of the greater diversity of generalist feeders in a more tropical region. *S.mauritianum* was uncommon further north in Natal and very few records were thus obtained there. No obviously important new species were thus added to the list of *S.mauritianum* herbivores.

*S.mauritianum* was common in the eastern Transvaal, particularly around Hazyview where it appeared to represent a problem in timber plantations. Plants examined in this area and in the Schoemanskloof pass were vigorous and showed very little signs of insect damage. Besides the usual generalist feeders, no important new herbivores were observed. Large quantities of fruit collected at Schoemanskloof also failed to yield any insects.

## 5.3. Insects associated with *S.hermannii*.

The herbivore community on Natal plants was very similar to that of the eastern Cape. Three new herbivores, the tortoise beetle (*Conchyloctenia hybrida* Boh.) and the ladybirds *Epilachna canina* Fabr. and *Epilachna paykulli* Muls. were encountered. In spite of the few plants encountered, most of the common herbivores of eastern Cape plants (Chapter 4) were observed. The pyraustids (*D.laisalis*), agromyzids (AcRh 467) and lonchaeids (*S. ophyroides*) were numerous.

Two of the three common herbivores of eastern Cape flowers, the gelechiids (*S* sp.nr. *concreta*) and the nitidulid beetles (*Pria* sp., AcRh 504) were encountered.

Slight differences were, however, noted between the folivores of Natal and eastern Cape *S.hermannii*. The most common eastern Cape folivores were the flea beetles (*Chaetocnema* sp., AcRh 465), tortoise beetles (*C.tigrina*) and epilachnine ladybirds (*H.hirta*). Flea beetles and ladybirds were seen in Natal. Although *C.tigrina* was not seen on *S.hermannii* in Natal, it was common on *S.panduriforme*, suggesting that it probably does attack *S.hermannii* here. The other tortoise beetle, *C.hybrida*, which occurs on *S.panduriforme*, was found on *S.hermannii* at Eshowe. Although *H.hirta* was recorded in Natal, it was not found inland north of Qumbu (Transkei) and Weza nearer the coast. *H.hirta* seemed to be replaced by another epilachnine, *E.canina* in northen Natal. Another species, *E.paykulli*, normally found on *S.panduriforme* in the region, was found on *S.hermannii* at Mapelane.

## 5.4. Insects associated with *S.panduriforme*.

The herbivore community in Natal and the Transvaal showed a degree of similarity with that of *S.hermannii* in the eastern Cape, although a number of differences were noted.

Twenty nine regularly-occurring phytophages were obtained (Table 5.1). On the foliage, the most numerous were the tortoise beetle (*C.tigrina*), epilachnine ladybird (*E.paykulli*) and flea beetle (*Chaetocnema* sp., AcRh 465). Other common herbivores included cicadellids (AcRh 530), leaf-galling cecidomyiids (AcRh 609) and buprestids (AcRh 540).

The folivores of *S.panduriforme* included a number of species previously collected on other species of *Solanum* in the eastern Cape. The tortoise beetle (*C.tigrina*), flea beetle (*Chaetocnema* sp., AcRh 465) and tip wilters (*Acanthocoris* sp., AcRh 553) were common on *S.hermannii*, *S.coccineum* and *S.rigescens*. Species previously found only on *S.coccineum* included the leaf-feeding noctuid (*P.* sp.nr.*diversipennis*), leaf-rolling caterpillar (AcRh 512) and tingid (*Urentius hystricellus* (Richter)).

Table 5.1. Major insect herbivores associated with *Solanum panduriforme* in Natal and the Transvaal. Species found only once excluded. *

| | *INCIDENCE* ** |
|---|---|
| *FOLIAGE* | |
| COLEOPTERA | |
| **Buprestidae (AcRh 540)** | 26,1 |
| **Chrysomelidae** | |
| Cassidinae (AcRh 621) | 4,4 |
| *Chaetocnema* sp. (AcRh 465) | 30,4 |
| *Conchyloctenia hybrida* Boh. | 13,0 |
| *Conchyloctenia tigrina* Oliv. | 39,1 |
| AcRh 626 | 4,4 |
| **Coccinelidae** | |
| *Epilachna canina* Fabr. | 4,4 |
| *Epilachna paykulli* Muls. | 39,1 |
| AcRh 534 | 4,4 |
| **Curculionidae** | |
| AcRh 622 | 4,4 |
| AcRh 623 | 4,4 |
| AcRh 627 | 4,4 |
| DIPTERA | |
| **Agromyzidae (AcRh 562)** | 8,7 |
| **Cecidomyiidae (AcRh 609)** | 26,1 |
| **Lonchaeidae (AcRh 610)** | 17,4 |
| HEMIPTERA | |
| **Cicadellidae (AcRh 530)** | 21,7 |
| **Coreidae** | |
| *Acanthocoris* sp. (AcRh 553) | 17,4 |
| **Fulgoridae (AcRh 624)** | 8,7 |
| **Lygaeidae** | |
| *Spilostethus* sp. (AcRh 501) | 8,7 |
| **Pentatomidae** | |
| AcRh 617 | 4,4 |
| **Tingidae** | |
| *Urentius hystricellus* (Richter) | 4,4 |
| LEPIDOPTERA | |
| **Leaf-roller caterpillar (AcRh 512)** | 13,0 |
| **Noctuidae** | |
| *Pardasena* sp.nr. *diversipennis* Gaede | 17,4 |
| | |
| *FRUIT* | |
| DIPTERA | |
| **Agromyzidae (AcRh 467)** | 20,0 |
| **Lonchaeidae** | |
| *Silba ophyroides* (Bezzi) | 80,0 |
| **Muscidae** | |

| | |
|---|---|
| *Atherigona* sp. (AcRh 470) | 20,0 |
| LEPIDOPTERA | |
| **Pyraustidae** | |
| *Daraba laisalis* (Walker) | 80,0 |
| | |
| *FLOWERS* | |
| COLEOPTERA | |
| **Nitidulidae** | |
| *Pria* sp. (AcRh 504) | 66,7 |
| LEPIDOPTERA | |
| **Gelechiidae** | |
| *Scrobipalpa* sp.nr. *concreta* (Meyrick) | 33,3 |

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* Voucher specimens of undetermined species lodged in the Albany Museum (Natural History), Grahamstown, South Africa.
** Percentage of the total number of samples in which the insects occurred.

The majority of the folivores of *S.panduriforme* had, however, not been encountered in the eastern Cape study. The most common of these were the ladybird (*E.paykulli*), leaf-galling cecidomyiid (AcRh 609), buprestid (AcRh 540), cicadellid (AcRh 530), leaf-galling lonchaeid (AcRh 610) and tortoise beetle (*C.hybrida*). The remainder were recorded in relatively low numbers.

The fruit were infested by the same species that attacked *S.hermannii*. These were the fruit-boring pyraustid (*D.laisalis*) and the lonchaeid (*S.ophyroides*), agromyzid (AcRh 467) and muscid (*Atherigona* sp., AcRh 470) flies. The flowers were similarly infested by the same species attacking *S.hermannii*, namely the gall-forming gelechiid (*S.* sp.nr. *concreta*) and the nitidulid beetle (*Pria* sp., AcRh 504). No new species were thus collected from the fruit and flowers of *S.panduriforme*.

## 5.5. Insects associated with *S.incanum*.

The herbivore list for this plant is incomplete, since relatively few samples were collected. Approximately 16 regularly-occurring phytophages were obtained (Table 5.2), the majority of which were also found on *S.panduriforme*. On the foliage, the most numerous were the flea beetle (*Chaetocnema* sp., AcRh 465), tortoise beetle (*C.hybrida*), epilachnine ladybird (*E.canina*) and the coreid

(*Acanthocoris* sp., AcRh 553). Two coreids (AcRh 555 and AcRh 556) were the only species not previously recorded on *S.panduriforme*.

Table 5.2. Major insect herbivores associated with *Solanum incanum* in Natal and the Transvaal. Species found only once excluded. *

| | *INCIDENCE* ** |
|---|---|
| *FOLIAGE* | |
| COLEOPTERA | |
| **Chrysomelidae** | |
| *Chaetocnema* sp. (AcRh 465) | 37,5 |
| *Conchyloctenia hybrida* Boh. | 25,0 |
| **Coccinelidae** | |
| *Epilachna canina* Fabr. | 25,0 |
| HEMIPTERA | |
| **Cicadellidae (AcRh 530)** | 12,5 |
| **Coreidae** | |
| *Acanthocoris* sp. (AcRh 553) | 25,0 |
| AcRh 555 | 12,5 |
| AcRh 556 | 12,5 |
| **Fulgoridae (AcRh 626)** | 12,5 |
| **Lygaeidae** | |
| *Spilostethus* sp. (AcRh 501) | 25,0 |
| **Pentatomidae** | |
| *Dryadocoris apicalis* (H.Sch) | 12,5 |
| **Tingidae** | |
| *Urentius hystricellus* (Richter) | 12,5 |
| *FRUIT* | |
| DIPTERA | |
| **Agromyzidae (AcRh 467)** | 33,3 |
| **Muscidae** | |
| *Atherigona* sp. (AcRh 470) | 33,3 |
| LEPIDOPTERA | |
| **Pyraustidae** | |
| *Daraba laisalis* (Walker) | 66,7 |
| *FLOWERS* | |
| COLEOPTERA | |
| **Nitidulidae** | |
| *Pria* sp. (AcRh 504) | +++ |
| LEPIDOPTERA | |
| **Gelechiidae** | |
| *Scrobipalpa* sp.nr. *concreta* (Meyrick) | +++ |

* Voucher specimens of undetermined specimens lodged in the Albany Museum (Natural History), Grahamstown, South Africa.
** Percentage of the total number of samples in which the insects occurred.
+++ Incidence not calculated due to insufficient samples.

Although samples of fruit and flowers of *S.incanum* were particuarly limited, virtually all species that infested fruit and flowers of *S.panduriforme* were collected. The gall-forming gelechiids (*S.* sp.nr. *concreta*) and nitidulids (*Pria* sp., AcRh 504) were noted on flowers, while the pyraustids (*D.laisalis*), agromyzids (AcRh 467), and muscids (*Atherigona* sp., AcRh 470) were reared from fruit. The lonchaeid, *S.ophyroides*, was the only species not collected from *S.incanum* fruit.

Although the assessment of the herbivore community of *S.incanum* is incomplete, it appears as if the herbivore fauna very closely matches that of *S.panduriforme*.

## 5.6. Discussion.

The status of *S.mauritianum* in Natal and the Transvaal did not appear to differ from the situation in the eastern Cape. The subtropical fauna comprised mainly polyphagous species and no species of importance were added to the list of insect herbivores in South Africa. The plants were hence vigorous and displayed a lack of obvious damage, like those of the temperate eastern Cape.

*S.mauritianum* thus appears to differ vastly from the indigenous species of *Solanum*, particularly as regards palatability to indigenous insect herbivores. Their unpalatability may well be based on strong anti-herbivore defences, since *S.mauritianum* foliage is densely trichomate and contains some highly toxic compounds (Van Dyck 1979), although failure of the herbivores to recognise the plant as a potential host is another possibility. The herbivore faunas of South African *Solanum* species appear not to be preadapted to utilize *S.mauritianum*, ensuring many vacant food niches on the plant. Zwölfer (1988) stressed the importance of local pools of preadapted herbivores in the evolution of thistle insect faunas. It thus seems unlikely that further collections on *S.mauritianum* in other climatic regions of South Africa will reveal any herbivores able to inflict appreciable levels of damage. The earlier suggestion (Chapter 3), that *S.mauritianum* is free of insect attack throughout South Africa and that biological control is a promising solution, seems thus to be confirmed.

The herbivore communities of *S.panduriforme* and *S.incanum* seemed similar to one another and had many species in common with *S.hermannii* in the eastern Cape. The fruit and flowers of all three species were attacked by the same herbivores, indicating the extensive range of these insects. Although the most common folivores of *S.hermannii* occurred on *S.panduriforme* and *S.incanum*, a greater number of folivorous species was collected on these two plants.

The diversity of insect species has been shown to follow a latitudinal gradient reflecting greater diversity towards the lower latitudes of the tropics (see Price 1984). This would imply an increase in the diversity of herbivores on *Solanum* species from temperate to more tropical areas. A comparison of the herbivore diversity of the indigenous *Solanum* species studied in temperate and subtropical regions is represented in Fig.5.3. Only regularly-occurring species (here taken as those occurring in at least 20% of the samples) were considered, in order to exclude occasional polyphagous feeders. *S.panduriforme* and *S.incanum*, which occupy mainly subtropical regions, displayed the greatest and second greatest diversity of species respectively. *S.incanum*, which was not sampled comprehensively, contained one more species than *S.hermannii*, which supported the greatest diversity of herbivores amongst temperate *Solanum* species. This may suggest that subtropical or tropical species of *Solanum* support a greater diversity of herbivores than temperate species.

There are, however, a number of factors which can influence the diversity of insect species on plants (Strong *et al.* 1984). Since different species of *Solanum* were studied in the two climatic regions, other factors besides climate may explain the apparent differences in herbivore diversity. A comparison of the same plant species in both regions could have provided a more conclusive result. However, *Solanum* species well represented in one region

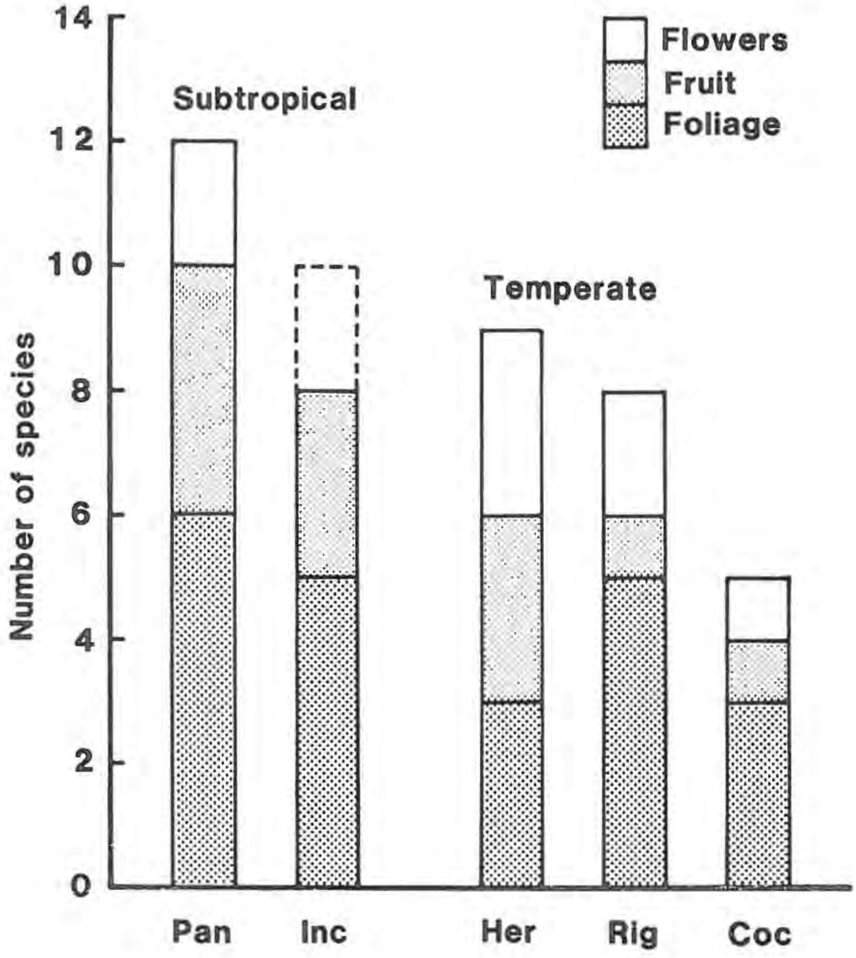

**Fig.5.3.** Insect herbivore diversity on indigenous *Solanum* species in subtropical and temperate regions. Only common species (those occurring in at least 20% of samples taken) are considered. Broken bars indicate species expected to occur commonly, but which were not confirmed due to lack of sufficient data. The species concerned were numerous on the other plant species on which they occurred. Pan= *Solanum panduriforme*, Inc= *Solanum incanum*, Her= *Solanum hermannii*, Rig= *Solanum rigescens* and Coc= *Solanum coccineum*.

were poorly represented in the other. *S.hermannii*, the only temperate species collected subtropically, could not be sampled comprehensively in the latter region because of its scarcity.

The subtropical fauna of *S.hermannii* did not appear to differ greatly from the temperate fauna. Although three new herbivore species were recorded on subtropical plants, these appeared to replace two of the most common temperate herbivores. The subtropical flora may, however, have been influenced by the effect of local abundance (Strong *et al.* 1984), which would have masked their possible potential for harbouring more herbivore species.

In summary, subtropical species of *Solanum* appear to harbour more herbivore species than those of temperate regions. However, since the same plant species could not be comprehensively sampled in both climatic regions, the factors causing these apparent differences could not be identified. The differences could thus be related to features of the plants and not the climatic regions.

# 6. GALL FORMATION ON *SOLANUM* SPECIES IN SOUTH AFRICA

## 6.1. Introduction.

Plant galls are an interesting aspect of insect-plant relationships and have been widely studied in terms of their morphological peculiarities (eg. Mani 1964) and evolutionary significance (eg. Price *et al.* 1987). Mani (1964) compiled an extensive catalogue, classifying plant galls and their causative agents, throughout much of the plant kingdom, although very little reference was made to *Solanum* species. A description of stem galls on *S.panduriforme* (Scholtz 1978, 1984) appears to be the only documented case of galling on *Solanum* plants in South Africa.

Surveys on the insect communities of some *Solanum* plants in the eastern Cape (Chapter 3) revealed the presence of two types of insect galls. These were flower galls on *S.hermannii* and stem galls on *S.coccineum* and *S.rigescens*. Collections in Zululand and the Transvaal (Chapter 5) revealed a further two types of galls on the leaves of *S.panduriforme*. These four *Solanum* species are listed as problem plants (Wells *et al.* 1986).

The four galls are described and biological data on the gall-forming insects and their natural enemies presented.

## 6.2. Flower galls on *S.hermannii*.

These were caused by caterpillars of the gelechiid *S.* sp.nr. *concreta* (AcRh 479) (Chapter 4). Galled flowers were abnormally large and failed to open, while the stamens were fused and thickened to form a hollow dome, in which the caterpillars developed (Fig.6.1a). The galls varied greatly in size, which was probably directly related to the maturity of both flowers and caterpillars. Galled flowers ranged in constant dry mass between 14 and 240mg (Mean=57,3mg: n=25) compared with a range of 5 to 49mg for normal flowers (Mean=21,1mg: n=25).

The caterpillars occurred singly, destroying the ovary during feeding and preventing fruit set. As previously recorded (Chapter 4), developing caterpillars changed colour from a dull transparent white to a bright red with two to four white transverse bands on the anterior region (Fig.6.1a). This may be an aposematic phase, since the caterpillars left the galls for pupation. Pupation probably occurred off the plant, since no coccoons were found on plants in the field. Apparently identical caterpillars (AcRh 573) destroyed the ovaries of flowers of *S.rigescens* and *S.coccineum* (Chapter 4) and moths reared from them were also identical. However, for unknown reasons, flowers of the latter two species did not show the swollen galled appearance, so that dissection was necessary to confirm caterpillar infestation.

Flower galls were common on *S.hermannii* throughout the eastern Cape. Although some galls occurred throughout the year, the extent of galling was seasonal (Chapter 4).

Two braconid parasitoids, *Apanteles* sp. (AcRh 477) and *Bracon* sp.1 (AcRh 510), were reared from the galls and appeared to attack the caterpillars. Small reddish ectoparasitic larvae were found attached to the exterior of some caterpillars. These were probably the larvae of *Bracon* sp.1, since southern African *Apanteles* species are all endoparasitoids (Prinsloo and Eardley 1985). Both braconids were solitary, since parasitised galls never yielded more than one parasitoid coccoon. A single individual of *Perilampus* sp. (Perilampidae; AcRh 608), which was possibly a hyperparasitoid (S.G. Compton pers.comm.), was also reared. The numbers of parasitoids reared in relation to numbers of moths is shown in Table 6.1. In order to determine the percentage parasitism, only galls where moth or parasitoid survival was demonstrated were considered; empty galls and those with dessicated caterpillars were excluded. From a total of 103 galls collected at different sites, 33% were parasitized. The parasitism was made up as follows: *Bracon* sp.1 (53%), *Apanteles* sp. (44%) and *Perilampus* sp. (3%).

Table 6.1. Numbers of *Scrobipalpa* sp.nr. *concreta* moths and parasitoids reared from the flower galls of *Solanum hermannii* in the eastern Cape.

| Locality | No.galls examined | No.moths emerged | No.parasitoids emerged | | |
|---|---|---|---|---|---|
| | | | Ap | Br | Pe |
| Grahamstown outskirts ($33^{o}19$'S $26^{o}31$'E) | 102 | 35 | 11 | 16 | 0 |
| Near Grahamstown ($33^{o}20$'S $26^{o}29$'E) | 27 | 5 | 1 | 0 | 0 |
| Keiskama River bridge ($33^{o}11$'S $27^{o}24$'E) | 54 | 23 | 3 | 2 | 1 |
| Cintsa Mouth ($32^{o}54$'S $28^{o}07$'E) | 10 | 3 | 0 | 0 | 0 |
| East London outskirts ($33^{o}01$'S $27^{o}02$'E) | 10 | 3 | 0 | 0 | 0 |

Ap *Apanteles* sp. (Braconidae) (AcRh 477)
Br *Bracon* sp.1 (Braconidae) (AcRh 510)
Pe *Perilampus* (Perilampidae) (AcRh 608)

## 6.3. Stem galls on *S.coccineum* and *S.rigescens*.

These were caused by an unidentified gelechiid (AcRh 480 and 481 from *S.coccineum* and *S.rigescens* respectively) (Chapter 3). The galls had a solid fusiform shape and bore numerous large thorns (Fig.6.1b). They were usually single-chambered, although galls containing up to three chambers have been found. In the latter, the chambers were isolated from each other (Fig.6.1c) and each, like the single-chambered galls, harboured a single caterpillar. The galls were 10-26mm in length (Mean=16,21mm: n=53) and 5-10mm in width (Mean=6,99mm: n=53). Similar galls formed by caterpillars were also collected from *Solanum tomentosum* L., although no moths emerged from these.

The developing caterpillars chewed away a small circular section of the gall wall, leaving only a thin external layer, through which the moths emerged. This behaviour occurs in most galls formed by Lepidoptera (Mani 1964). Prior to pupation, the caterpillars lined the gall chambers with silk and subsequently pupated with their

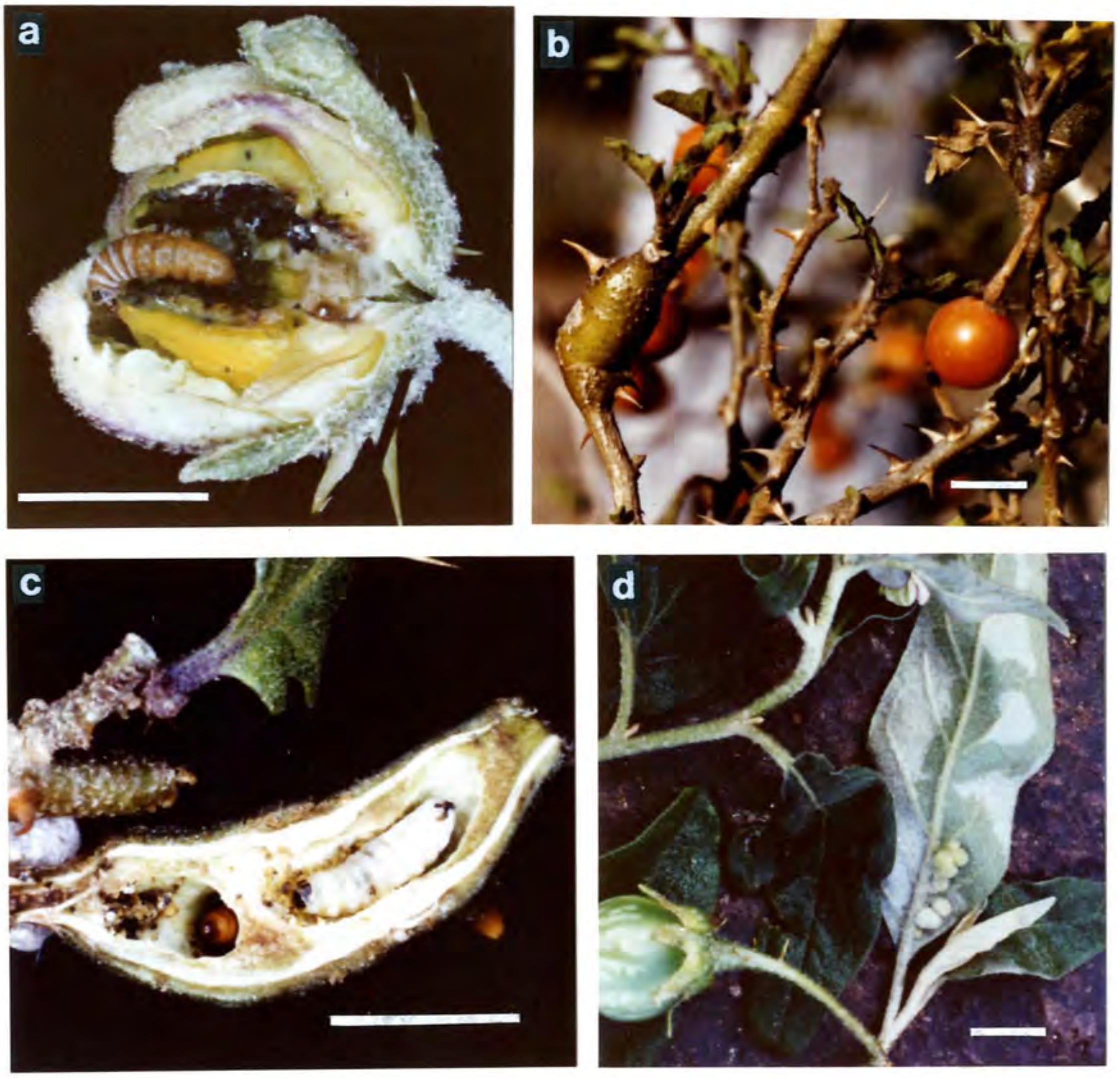

**Fig.6.1.** Galls associated with *Solanum* (scale line= 10mm). a. Flower gall of *Scrobipalpa* sp.nr. *concreta* on *Solanum hermannii* showing the enlarged fused stamens and damaged ovary. b. Fusiform stem galls of the gelechiid moth (AcRh 481) on *Solanum rigescens*. c. As for (b); multi-chambered gall split open to show a caterpillar (parasitized) and a pupa in separate chambers. d. Clusters of simple leaf galls of the cecidomyiid (AcRh 609) on the undersurface of a leaf of *Solanum panduriforme*.

heads facing the exit. The emerging moths were thus channelled by their coccoons towards the exit. The ruptured "escape window" and presence of scales around the exit was evidence of emergence by a moth. Moths were occasionally found trapped inside the galls. This means of escape from the gall differed from that of the gelechiid, *Scrobipalpa incola* (Meyrick), which galls the stems of *S.panduriforme* (Scholtz 1978, 1984). These galls dehisced by a circular stopper-like lid which fell off leaving a hole for emergence.

The only visible difference between occupied galls and old galls was the presence of emergence holes in the latter. The moths had a shiny golden lustre and were cryptic against the thorny stems of the plants.

The galls were relatively localised but often occured in large numbers on individual plants. An examination of 30 *S.coccineum* plants, growing along a 30m section of fence near Tarkastad, showed that only 8 plants (27%) contained at least one gall. Similarly, in an examination of 30 *S.rigescens* plants growing together near Port Alfred, only three plants (10%) were galled. The fact that galls were often very numerous on a particular plant, may have been due to emerging moths remaining and ovipositing on the same plant. Moths that emerged in the laboratory remained at least during the day on the galled twig, upon which they are effectively camouflaged, and were not found sitting on the container walls. There is a further possibility of variation in susceptibility amongst the individual plants.

Four hymenopterous parasitoids were reared from the galls, and all appeared to attack the caterpillars. An *Apanteles* sp. (Braconidae; AcRh 496) and *Eurytoma* sp.1 (Eurytomidae; AcRh 499) emerged from both *S.coccineum* and *S.rigescens* galls. A species of *Physaraia* (Braconidae; AcRh 494) and an ichneumonid (AcRh 473) were obtained only from galls of *S.rigescens* and *S.coccineum* respectively. All parasitoids appeared to be solitary. The frequency of parasitoids in relation to moths is shown in Table 6.2. Percentage parasitism

Table 6.2. Numbers of gelechiid moths and parasitoids reared from stem galls of *Solanum coccineum*, *S.rigescens* and *S.tomentosum* in the Cape Province.

| Locality | No.galls examined | No.moths emerged | No.parasitoids emerged | | | |
|---|---|---|---|---|---|---|
| | | | Ap | Eu | Ic | Ph |
| *S.coccineum* | | | | | | |
| Near Bedford<br>(32°45'S 26°06'E) | 91 | 60 | 9 | 16 | 0 | 0 |
| Grahamstown outskirts<br>(33°17'S 26°29'E) | 30 | 6 | 6 | 0 | 12 | 0 |
| Near Graaff-Reinet<br>(32°17'S 24°30'E) | 23 | 8 | 2 | 5 | 0 | 0 |
| Near Tarkastad<br>(31°50'S 26°17'E) | 10 | 0 | 0 | 2 | 0 | 0 |
| *S.rigescens* | | | | | | |
| Near Grahamstown<br>(33°21'S 26°29'E) | 14 | 10 | 1 | 0 | 0 | 1 |
| Grahamstown outskirts<br>(33°19'S 26°32'E) | 22 | 7 | 0 | 1 | 0 | 2 |
| Near Bathurst<br>(33°27'S 26°47'E) | 30 | 7 | 8 | 1 | 0 | 5 |
| Port Alfred<br>(33°35'S 26°53'E) | 16 | 9 | 3 | 0 | 0 | 0 |
| *S.tomentosum* | | | | | | |
| E of Montagu<br>(33°45'S 20°28'E) | 12 | 3 | 0 | 4 | 0 | 0 |

Ap *Apanteles* sp. (Braconidae) (AcRh 496)
Eu *Eurytoma* sp.1 (Eurytomidae) (AcRh 499)
Ic Ichneumonidae (AcRh 473)
Ph *Physaraia* sp. (Braconidae) (AcRh 494)

was again calculated, with the exclusion of empty galls and those with dessicated caterpillars. From a total of 126 galls collected from *S.coccineum* at different sites, 41% were parasitised. The parasitism was made up as follows: *Eurytoma* sp. (44%), *Apanteles* sp. (33%) and the ichneumonid (23%). Similarly, a sample of 55 galls collected from *S.rigescens* showed that 40% were parasitised. This parasitism was made up as follows: *Apanteles* sp. (55%), *Physaraia* sp. (36%) and *Eurytoma* sp.1 (9%). Emerging parasitoids chewed tiny holes in the "escape window" made by the caterpillars, while emerging moths ruptured the entire "window". Old parasitized galls could thus be distinguished from non-parasitized galls by the emergence holes.

## 6.4. Simple leaf galls on *S.panduriforme*.

These were small nodular structures, 2-4mm in size, which occurred in clusters mainly on the undersurfaces of the leaves (Fig.6.1d). In the samples examined, galls were often situated along the midribs and major veins of the leaves. They had a hairy appearance, due to a covering of leaf trichomes which was denser than on the remainder of the leaf surface. The galls were often numerous, with up to 40 concentrated on a leaf. The galls were single-chambered.

These nodules were caused by a gall midge (Cecidomyiidae; AcRh 609). Few midges were reared, since the galls were heavily parasitised (Table 6.3). Parasitoids comprised a eurytomid (*Eurytoma* sp.2; AcRh 612) and a braconid (*Bracon* sp.2; AcRh 614). *Eurytoma* sp.2 comprised 84% of the parasitoids reared and *Bracon* sp.2 the remaining 16%.

Table 6.3. Numbers of flies and parasitoids reared from two types of leaf galls on *Solanum panduriforme* in the Transvaal and Natal.

| Locality | No. flies emerged | No. parasitoids emerged | | | |
|---|---|---|---|---|---|
| | | Ea | Ey | Bn | Cy |
| **Simple leaf galls** | | | | | |
| Mkuzi River<br>(27°36'S 32°13'E) | 0 | 38 | - | 0 | - |
| S of Mbazwana<br>(27°29'S 32°35'E) | 1 | 0 | - | 6 | - |
| Nr. Nkwalini<br>(28°43'S 31°31'E) | 0 | 13 | - | 4 | - |
| Masalal<br>(22°44'S 30°48'E) | 12 | 0 | - | 0 | - |
| **Compound "puff galls"** | | | | | |
| E of Mapelane<br>(28°24'S 32°20'E) | 6 | - | 9 | 1 | 7 |

Ea *Eurytoma* sp.2 (Eurytomidae) (AcRh 612)
Ey *Eurytoma* sp.3 (Eurytomidae) (AcRh 613)
Bn *Bracon* sp.2 (Braconidae) (AcRh 614)
Cy Cynipidae (AcRh 611)

## 6.5. Compound "puff galls" on *S.panduriforme* leaves.

These compound structures often comprised numerous rounded units. They were variable in size, varying between 11 and 23mm in width and 11 and 42mm in length. The galled part of the leaf was thickened, distorted and woody and was covered by a dense layer of long trichomes. This layer was composed of abnormally long trichomes, 3-6mm in length, which increased the apparent size of the galls and conferred a "puff-ball" appearence (Fig.6.1e,f).

The galls were multi-chambered with numerous isolated chambers in the woody part of the leaf, separated by a pulpy material. The galls were caused by a lonchaeid fly (AcRh 610), identified as a species of *Lamprolonchaea* according to a key by McAlpine (1960). Three species of parasitoid were reared, and were numerous in comparison to the number of flies (Table 6.3). They comprised a braconid (*Bracon* sp.2; AcRh 614), eurytomid (*Eurytoma* sp.3; AcRH 613) and a cynipid (AcRh 611). *Bracon* sp.2 appeared to be the same species as that reared from the simple leaf galls, while the species of *Eurytoma* was different. The eurytomid and cynipid were equally abundant, while only a single braconid was reared.

## 6.6. Discussion.

Two main hypotheses have been advanced to explain the relationship between gall-forming insects and their host plants (Mani 1964). The first regards the insect-plant relationship as one of parasitism, whereby the insect induces and then exploits a physiological response of a plant. However, Mani also pointed out that a gall localises a parasite in space and time, imposing a highly specialized lifestyle. The second hypothesis thus regards gall formation as a defensive strategy by the plant to minimize the negative effects of parasitism. The adaptive significance of insect gall formation was reviewed by Price *et al.* (1987). The plant-protection hypothesis proposed by Mani was rejected, since galls clearly showed adaptive features for the insect and not the plant. The thick fibrous layer of the *S.panduriforme* "puff galls" supports

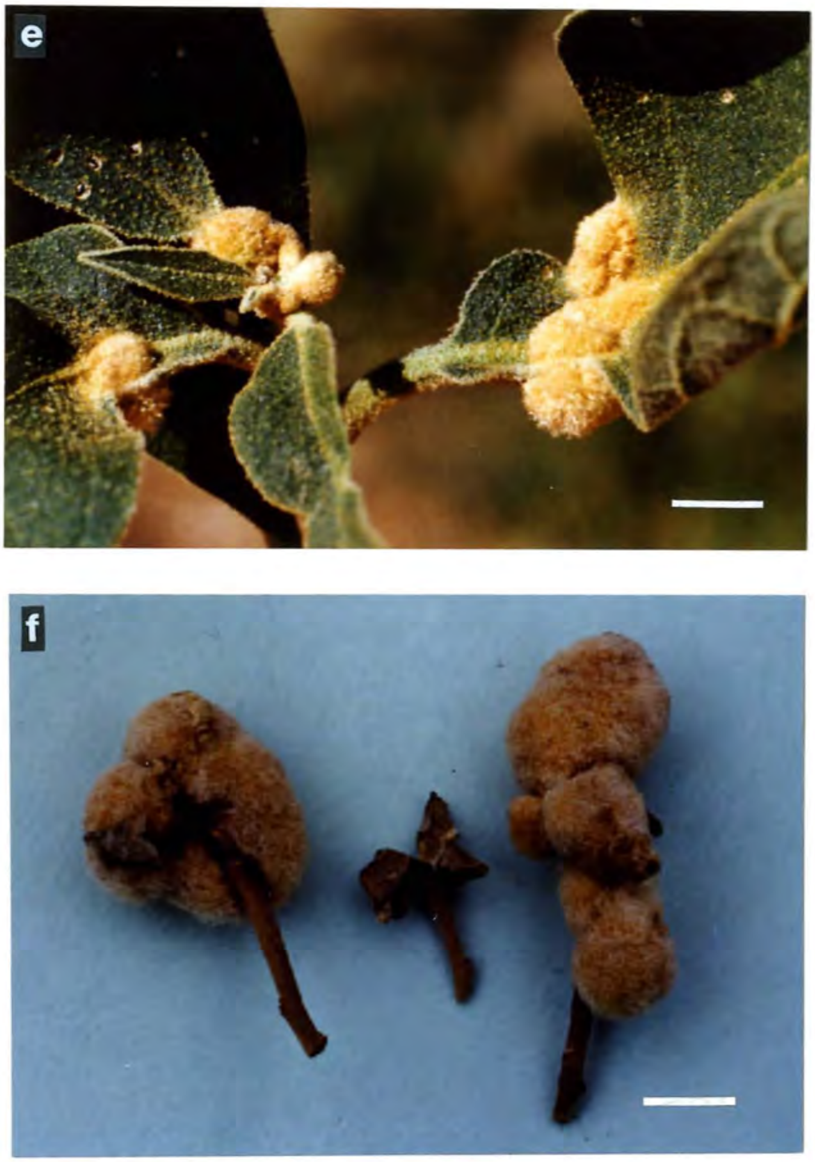

**Fig.6.1. continued.** e. Small compound leaf galls ("puff galls") of the lonchaeid (AcRh 610) on the leaves of *Solanum panduriforme*. f. Large "puff galls" with trichomes removed from the middle one to show the galled woody remains of two leaves.

the latter conclusion. The layer has no possible function in containing the gall-former, but may rather protect the gall-former's larvae from parasitism. In a study of tenthredinid sawflies, Price and Pschorn-Walcher (1988) showed that gall-formers supported fewer parasitoid species than exposed feeders and were thus better protected. These authors suggested that natural enemies may have been important as a selective factor in the evolution of gall formation amongst, at least, sawflies.

In South Africa, gall formers have been shown to suppress growth and reduce the reproductive potential of weeds like *Hypericum perforatum* L. (Gordon and Neser 1986) and *Acacia longifolia* (Andr.) Willd. (Dennill 1988). The potential of gall formers in biocontrol has, however, been underrated (Harris 1973) because of their indirect effects on plant fitness. The four galls described may have a negative influence on the fitness of their hosts, since many galls act as sinks for essential nutrients (Price *et al.* 1987). However, Gandar (1979) calculated that gelechiid galling of the stems of *S.panduriforme* caused a loss of only 6% of the biomass and had very little effect on plant vitality. The flower galls of *S.hermannii* seem likely to cause a significant nutrient-drain on the plant since they are, in terms of dry mass, on average three times the size of normal flowers. In addition, the caterpillars of *S.*sp.nr. *concreta* destroy the ovaries directly, creating a double negative effect on the reproductive output of *S.hermannii*. In this respect their influence is similar to that of the pteromalid wasp, *Trichilogaster acaciaelongifoliae* Froggatt, which galls the reproductive buds of *A.longifolia* (Dennill 1988). The effects of the stem and two leaf galls are more difficult to assess, since they are not as direct as that of the flower galls. It is possible that the leaf galls, in particular the compound "puff galls", cause some reduction in the photosynthetic capability of *S.panduriforme* foliage. The ultimate influence of the four galls on the growth and reproduction of their hosts can only be determined by extensive field and experimental studies. The gall formers could possibly be regarded as useful natural enemies, in the light of the minor weed status assigned to their *Solanum* hosts.

# 7. BIOLOGY AND *SOLANUM* HOST RANGE OF *C.TIGRINA*

## 7.1. Introduction.

The tortoise beetles (Cassidinae) are a large subfamily of phytophagous beetles, which is represented by about 16 genera and 90 species in southern Africa (Endrödy-Younga 1985). Little has been published on the biology of southern African Cassidinae, possibly because of their low pest status, there being only two recorded cassidine pests of cultivated crops in southern Africa (see Annecke and Moran 1982). The status of tortoise beetle taxonomy in southern Africa is thus poor, the most recent published work being a key to the tribes of Cassidinae by Hincks (1952).

Adults and late instar larvae are voracious feeders and according to Paterson (1941) may affect the population densities of their host plants. Two Argentinian species, *G.lutescens* and *G.pallidula* (Boh.), were considered as possible control agents for the exotic *S.elaeagnifolium* (silverleaf nightshade, satansbos) in South Africa (Siebert 1975).

*C.tigrina*, illustrated by Muir and Sharp (1904), is commonly associated with indigenous *Solanum* plants in the eastern Cape and at high densities is able to skeletonize leaves (Chapter 4). A study of the biology and host range of *C.tigrina* was undertaken as a contribution toward achieving a greater understanding of the indigenous herbivores of *Solanum* species.

## 7.2. Life cycle and biology.

### *a. Egg.*

The eggs were enclosed in cases (oothecae), which were attached to the undersides of leaves, usually against the veins (Fig.7.1a,b). Egg cases show much morphological variation within the Cassidinae (Muir and Sharp 1904). The egg cases of *C.tigrina* were consistent with the description of them by Muir and Sharp (1904) and were very

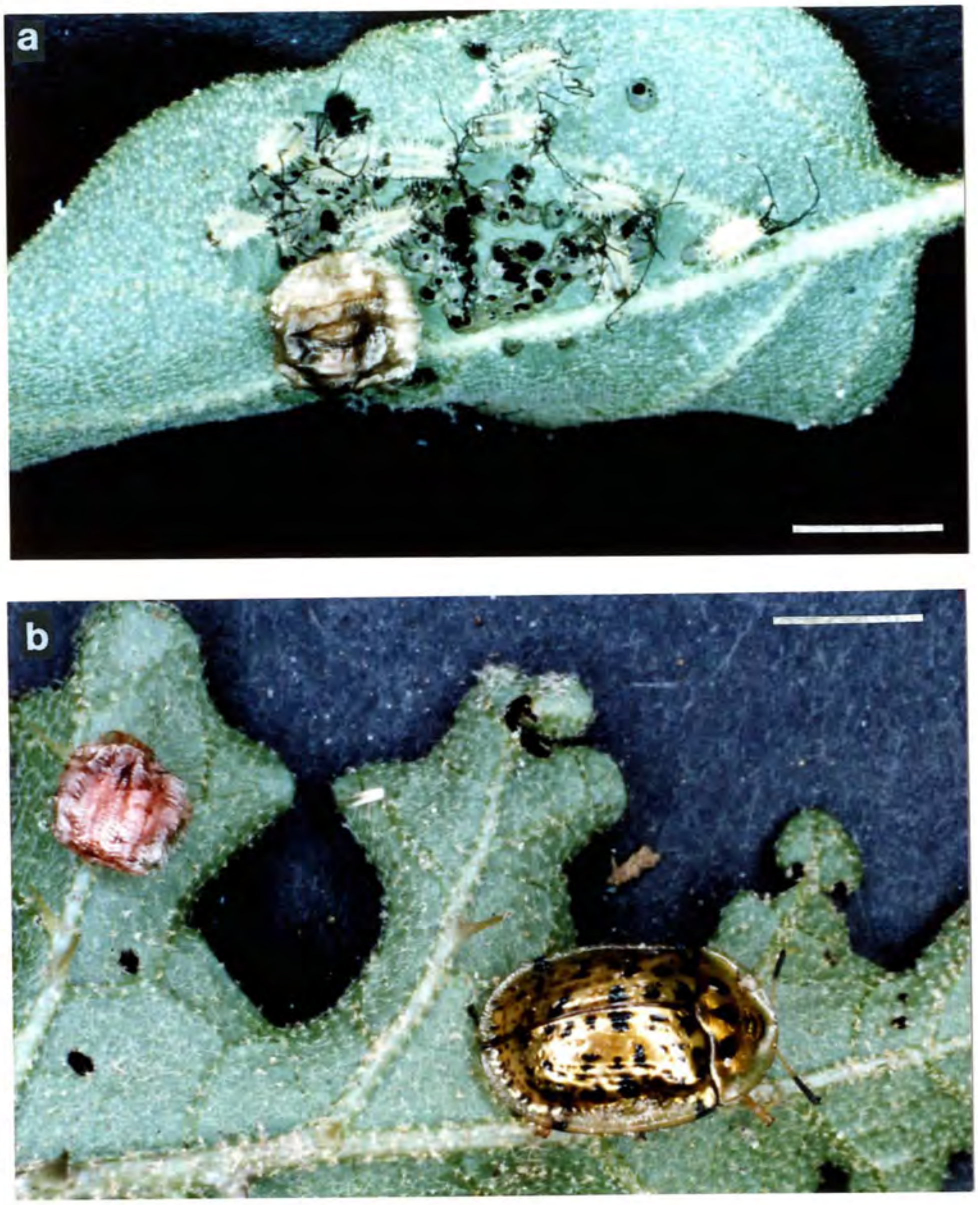

**Fig.7.1.** *Conchyloctenia tigrina* (scale line= 5mm). a. Egg case and newly emerged first instar larvae on a leaf of *Solanum coccineum*. The areas cleared of trichomes by the larvae, prior to feeding, are visible. b. Mature adult showing the characteristic golden lustre and black speckling and a newly-oviposited egg case.

similar to those of *C.hybrida* (Paterson 1941) and *G.lutescens* (Siebert 1975). The egg cases comprised vertically stacked transluscent membranes, joined at the edges on one side. Between each two membranes there was a single egg, situated approximately in the centre. The top 2-3 membranes had no eggs and probably served to protect the underlying eggs. The number of eggs per case ranged from 2-18, with a mean of 7,62 ± 0,05 (Mean ± SE).

In a sample of 50 egg cases from the laboratory culture, the mean length was 4,65 ± 0,04mm and the mean width 4,19 ± 0,08mm. The incubation period ranged from 227-298 hours, with a mean of 264,45 ± 2,08 hours (11,02 days). The percentage of eggs that hatched was 81,4. Of those that did not hatch, 10,5% developed but failed to hatch and 8,1% failed to develop at all.

### *b. Larva.*

The morphology of the larva was described by Muir and Sharp (1904) and is typical of other members of the subfamily (see Skaife 1979). The colour varies from light yellow to green. Old larval skins and excreta are packed onto the caudal process where they form a solid blackish mass. The larval instar can thus be determined simply by counting the head capsules on the larval skins. Siebert (1975) suggested that this arrangement served to camouflage the larvae of *G.lutescens*. However, the black caudal mass is conspicuous against the paler colour of *C.tigrina* larvae. The arrangement may have a defensive function, in that disturbed larvae flex their posterior abdominal regions bringing the caudal mass towards the head. Skaife (1979) suggested that this behaviour in larvae of *Aspidomorpha* species may dislodge predators or direct their attention away from the larvae. The caudal mass may also have a sanitary effect, in that the excreta collects on the caudal process and does not come into contact with the food (Skaife 1979).

Apart from size and the number of larval skins on the caudal process, there appear to be no external morphological differences between the five instars. Larval size ranged from 1-2mm in the first instar to 6-8mm in the mature fifth instar (Figs.7.2a,b). Owing to the overlap of both total length and head capsule width of the different instars, size cannot be used to separate them. The lower mean head capsule width of the prepupae relative to the fifth instars (Fig.7.2b) was unusual. Since no moult occurs between these two stages, the head capsule widths should be very similar. However, a Mann-Whitney comparison showed no significant difference ($p>0,05$) between the two stages.

The duration of the five instars, including the prepupal phase, was approximately 28 days. The duration of the first three instars was similar, each lasting approximately four days (Fig.7.2c). The fourth and fifth instars took longer, approximately five and eight days respectively. The mature fifth instar larvae underwent a non-feeding sessile phase prior to pupation, which lasted between two and three days. These prepupae were attached midventrally by means of a secretion to the leaf undersurface. This prepupal phase was recorded by Paterson (1941) for *Aspidomorpha tecta* Boh. and Siebert (1975) for *G.lutescens*.

Larvae fed on the surfaces as well as the edges of the leaves. Early instars seemed to feed more on the surface and later instars on the edges. Larvae feeding on the flat surfaces bite off the star-shaped trichomes which characterize *Solanum* leaves, before they feed. The resulting "shaved" patches were particularly conspicuous on *S.coccineum*, which has a high density of leaf trichomes (Fig 7.1a). This mowing of trichomes prior to feeding has previously been found in caterpillars of *P.* sp.nr. *diversipennis* (Noctuidae) feeding on *S.coccineum* (Hulley 1988). The larvae, particularly the later instars, are voracious feeders and at high densities may skeletonize leaves. Abscission of badly damaged leaves was observed on potted plants.

### *c. Pupa.*

The pupae were morphologically similar to the larvae and were consistent with the description given by Muir and Sharp (1904). The

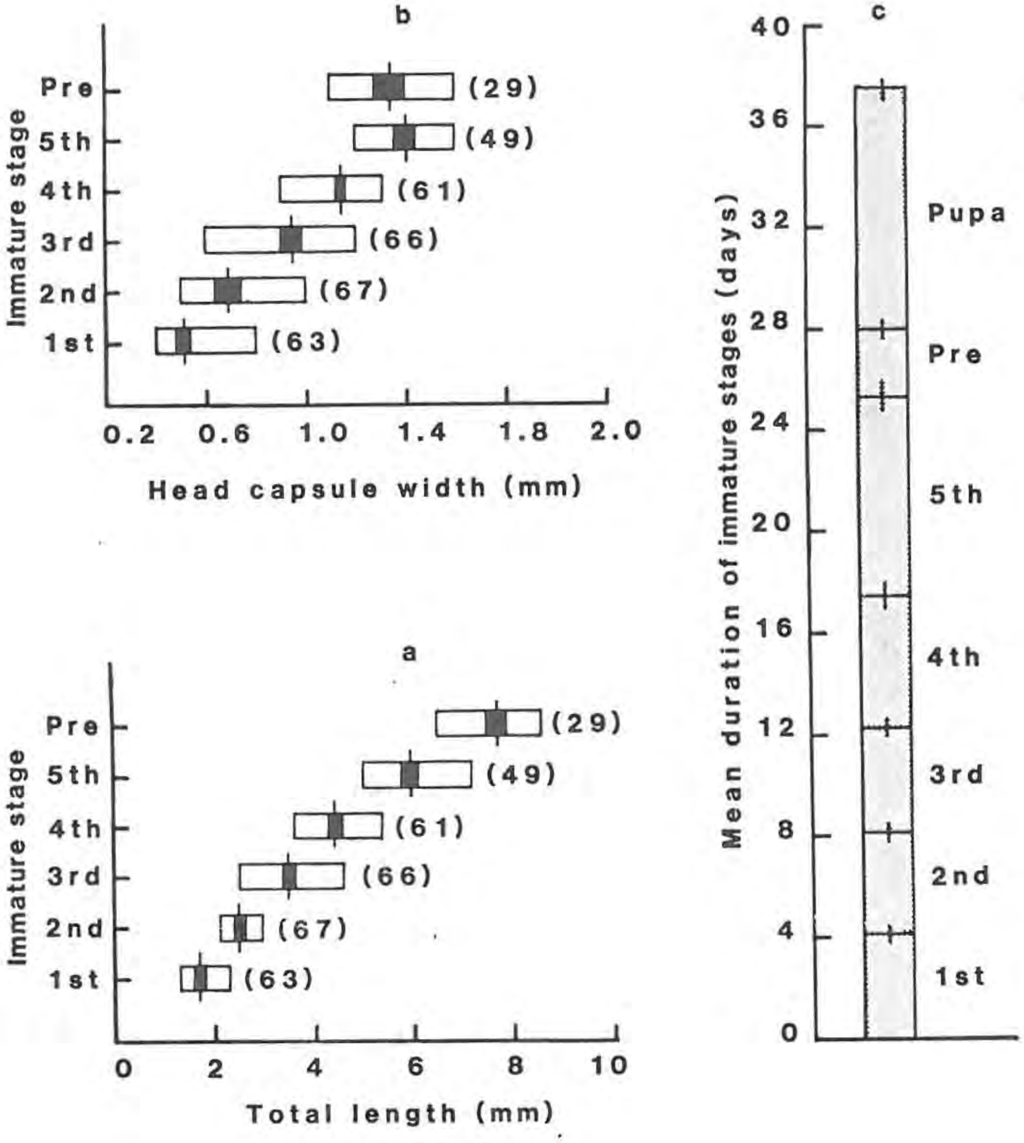

Fig.7.2. Size and duration of the immature stages of *Conchyloctenia tigrina* on *Solanum hermannii* in the laboratory. a. Total length and (b) head capsule width of the larval and prepupal stages (the horizontal bars, vertical lines and shaded areas represent the ranges, means and two standard errors of the mean respectively; the numbers in parentheses indicate the number of samples). c. The mean duration of the larval, prepupal and pupal stages (the vertical lines represent two standard errors of the means).

colour varied from green to yellow, with a dorso-lateral black stripe. The pronotum, which conceals the head, is expanded as a smooth shield, bearing fine spines. On each side of the abdomen are five lateral triangular projections, each bearing short slender spines.

The pupae varied in length from 6 to 8mm with a mean of 7,20 ± 0,14mm and the pronotal width varied from 5 to 6mm with a mean of 5,40 ± 0,07mm. The duration of the pupal stage was approximately 10 days (Fig.7.2c).

### *d. Adult.*

On emergence, the teneral adults are pale yellow with black speckling on the elytra. The pronotum bears three large black spots, which lie parallel to the junction between the pronotum and the elytra. The maturing beetles eventually develop an attractive golden lustre (Fig.7.1b), caused by reflection and interference of light reaching different layers of cuticle (Neville 1977, Skaife 1979). The golden lustre fades soon after death, but is restored if the beetles are rehydrated in a relaxing chamber.

In both laboratory-reared and field-collected (Fig.7.3) beetles, the females were significantly larger than the males (t= 13,9, p<0,0001; t=15,1, p<0,0001 respectively), although considerable overlap occurred. The sex of the measured beetles was confirmed by dissection, as the sexing of living tortoise beetles is uncertain (Siebert 1975, Ward and Pienkowski 1978a). Field-collected females were on average 10,24 ± 0,05mm long (n=54) and males on average 9,22 ± 0,05mm (n=46).

A sample of 100 field-collected beetles contained 46 males and 54 females. The ratio was not significantly different from equality ($\text{Chi}^2_{[1]}$= 0,64; p> 0,05). This result was confirmed in the lab where, coincidentally, an identical ratio was obtained.

The adults, like the larvae, fed on the flat surfaces or edges of

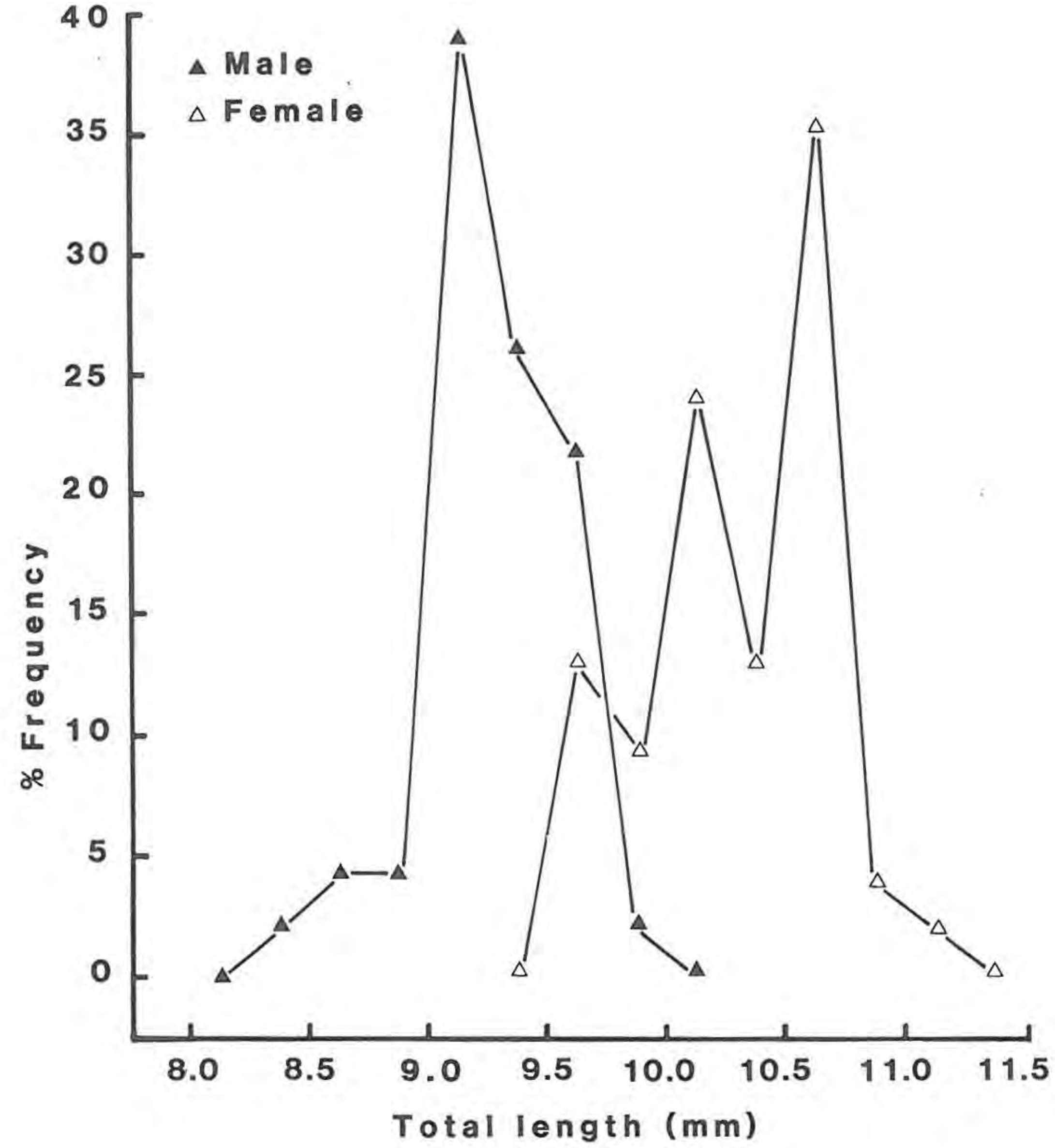

**Fig.7.3.** Frequency polygons of the body lengths of field-collected male and female *Conchyloctenia tigrina* adults.

the leaves. Leaf trichomes were bitten off prior to feeding on the flat surfaces. This behaviour was inferred by Siebert (1975) for adults of *G.lutescens* feeding on *S.elaeagnifolium*, from the presence of "fluff" at the bottom of the cages. At high adult population densities, leaves were skeletonized by feeding damage, both in the laboratory and field.

### *e. Parasitoids.*

Egg cases collected from *S.hermannii* and *S.rigescens* in the field were parasitized by a species of *Tetrastichus* (Eulophidae) (Chapter 4). In a sample of 88 egg cases collected from *S.hermannii* 65,9% contained at least one parasitized egg. Parasitized cases were identified by the round exit holes in the egg case membranes made by the emerging wasps. The parasitism rate for individual eggs was determined from a sample of twelve egg cases containing a total of 117 eggs. In this sample, 38,5% of the eggs were parasitized by *Tetrastichus* sp. Species of *Tetrastichus* have been recorded as egg parasitoids of two tortoise beetles, *Cassida indicola* Duv. and *Aspidomorpha indica* Boh., attacking field-bindweed in Pakistan (Balloch 1977).

No parasitoids were obtained from field collected larvae, both prior to and after pupation. The pupae were parasitized by an unidentified chalcidid wasp (Chapter 4). These emerged as solitary adults from pupae collected on *S.hermannii*, *S.rigescens* and *S.panduriforme*. The latter plant species was sampled in Zululand and Zimbabwe. Parasitized pupae were characterized by a dark brownish colour. The wasps emerged leaving a large round hole on the dorsal or the ventral surface of the abdomen. In a sample of 31 pupae collected from *S.hermannii*, 38,7% were parasitized by the chalcidid. In addition, a single unidentified ichneumonid was reared from a pupa collected from *S.hermannii*. Another chalcidid, *Spilochalcis albifrons* (Walsh), parasitized the pupae of the thistle-feeding tortoise beetle, *Cassida rubiginosa* Muller, in North America (Ward and Pienkowski 1978b). Siebert (1975) mentioned unidentified eulophids which parasitized *C.tigrina* pupae collected on *S.panduriforme*. None of these appeared in our samples.

## 7.3. Annual cycle.

*C.tigrina* reared on *S.hermannii* in the laboratory took approximately 38 days to develop from egg to adult (Fig.7.2c). Beetles were found in the field for about eight months during the year, so that a number of generations a year is possible. Two generations a year are typical of Cassidinae, with overwintering in the adult stage (Paterson 1941). Overwintering coincides with the onset of colder weather, shorter day lengths and a possible reduction in the nutritional quality of the host plants. At Grahamstown, overwintering occurred from May to the end of August. The first adults were seen from the beginning of September, more or less coinciding with the first occurrence of warm weather, and were assumed to be from the overwintering population. It is not known where *C.tigrina* adults overwinter, since searches of leaf litter and debris at the base of the plants did not reveal any adults.

Day length appears to be important in initiating mating and/or oviposition, since oviposition did not occur in the laboratory under a 12 hour photoperiod, but was induced when the day length was increased to 16 hours. The above experiment was carried out in summer. In winter, under the same temperature conditions, a photophase of 16 hours was ineffective in inducing oviposition. This may indicate that the plants collected as food for the beetles in winter may have been suboptimal in some respect, or that a climate induced diapause was operating.

## 7.4. Host range.

### *a. Field observations.*

At various field sites in the eastern Cape, the beetles fed and oviposited on *S.hermannii*, *S.rigescens* and *S.coccineum*, but not on the exotic *S.mauritianum*. Egg cases and beetles were also collected from *S.panduriforme* in Zululand and Zimbabwe and from *S.incanum* in the north-eastern Transvaal. Although not recorded as a pest of cultivated eggplant (*S.melongena*), oviposition and subsequent larval feeding was observed on this plant in a garden in Grahamstown where wild solanums were in close proximity. Extensive defoliation was observed in this case.

### *b. Laboratory survival tests.*

The mortalities and life cycle durations of larvae fed on *S.hermannii*, *S.coccineum*, *S.elaeagnifolium* and *S.rigescens*, are shown in Fig.7.4. *S.mauritianum* was included in the test but results are excluded from Fig 7.4, since all larvae had died by the second instar and life cycle duration could thus not be measured.

Mann-Whitney comparisons of the mortality of the immature stages showed that mortality was significantly lower ($p<0,05$) on each of the indigenous *S.hermannii*, *S.rigescens* and *S.coccineum* relative to either of the exotics, *S.mauritianum* and *S.elaeagnifolium*. No reliable statistical comparisons could be made between the life cycle durations of larvae reared on indigenous and exotic species, due to the high mortalities on the exotic species. Although overall mortality was not significantly different on *S.mauritianum* and *S.elaeagnifolium* ($p>0,05$), the larvae survived for far longer on the latter. Possible explanations for host unsuitability include leaf trichomes, secondary plant chemicals and unsuitable nutritional characteristics of the plants.

On the densely trichomate leaves of *S.mauritianum*, the energy expenditure involved in trichome clearing may have been too great. The larvae, none of which survived beyond the second instar, had cleared only very small areas on the leaves, suggesting that starvation was the major cause of mortality. The role of secondary chemicals remains unknown.

On the less hirsute *S.elaeagnifolium*, first and second instar mortality was 2% and 18% respectively and was much lower relative to the 92% and 100% mortality of *S.mauritianum* first and second

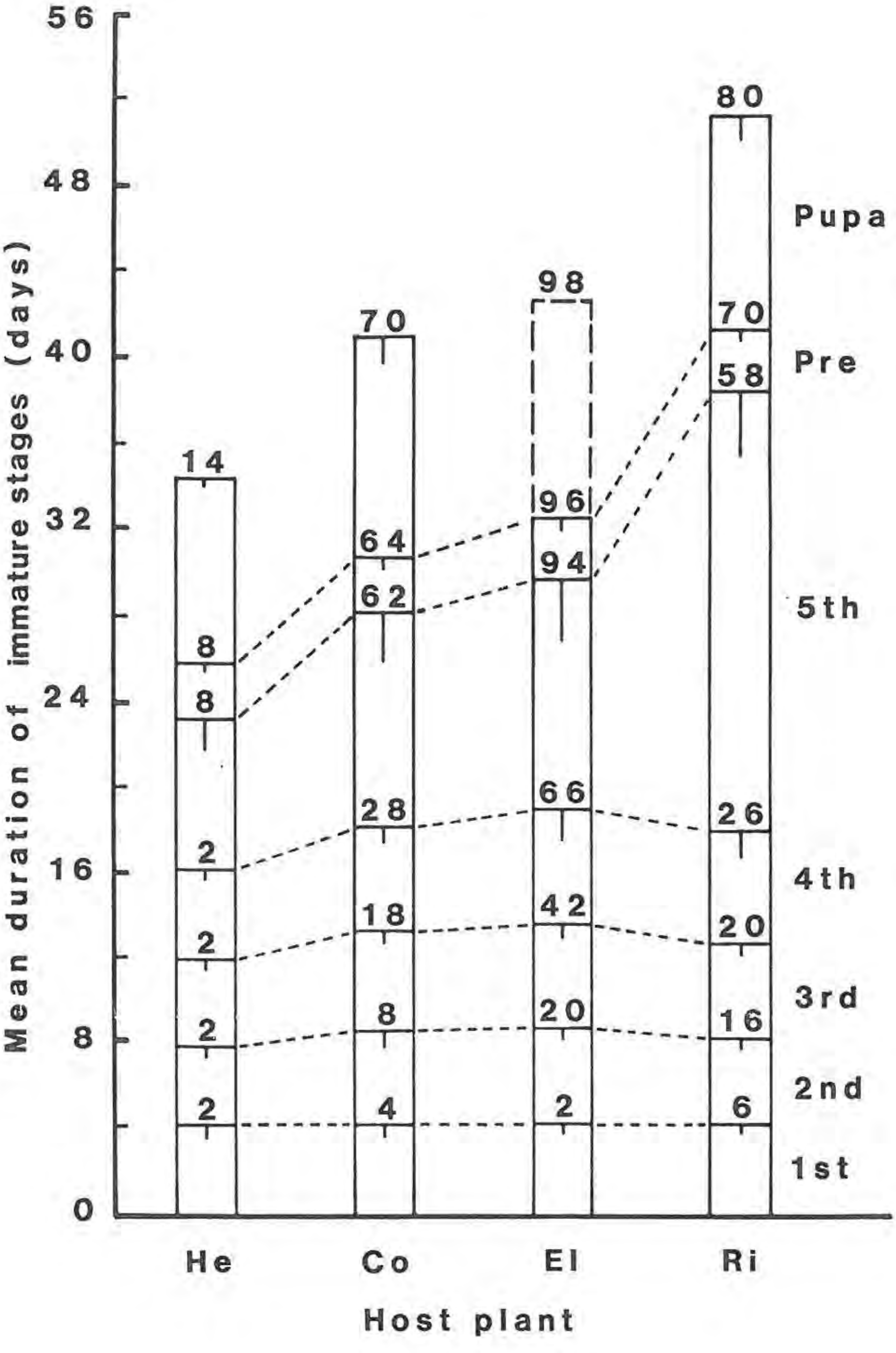

Fig.7.4. Mean duration and survival of the immature stages of *Conchyloctenia tigrina* reared on *Solanum hermannii* (He), *Solanum coccineun* (Co), *Solanum elaeagnifolium* (El) and *Solanum rigescens* (Ri). The vertical bars represent two standard errors of the mean and the numbers above the bars indicate the cumulative percentage mortality at the end of each stage.

instars. However, mortality increased rapidly over subsequent instars to reach 98% by the pupal stage. The fact that larval mortality took longer to manifest itself than on *S.mauritianum* and was higher than in the more densely trichomate *S.coccineum* may suggest that nutrition or secondary chemical toxicity is the major cause of mortality on *S.elaeagnifolium*.

Mann-Whitney comparisons between the indigenous plants showed that *C.tigrina* larvae reared on *S.hermannii* suffered significantly lower mortality (p<0,05) and completed their life cycle in a significantly shorter time (p<0,05) than those reared on either *S.coccineum* or *S.rigescens*. Although there was no significant difference in immature stage mortality (p>0,05) between *S.coccineum* and *S.rigescens*, larvae reared on *S.coccineum* completed their life cycle in a significantly shorter time (p<0,05) than those on *S.rigescens*. *S.hermannii* thus appears to be the most suitable of the indigenous plants tested. The apparent unsuitability of *S.coccineum* may relate to the dense trichome layer, which makes larval feeding energetically demanding, perhaps in addition to other factors. The relative unsuitability of *S.rigescens* may be due to chemical or nutritional factors since its trichome layer approximates that of *S.hermannii* in density.

# 8. DIFFERENTIAL INFLUENCES OF TWO HOST PLANTS ON THE FITNESS OF *C.TIGRINA*

## 8.1. Introduction.

The biology and host range of the oligophagous tortoise beetle, *C.tigrina* was discussed in Chapter 7. Survival tests in the latter study showed that larvae of beetles, collected on *S.hermannii*, suffered higher mortality and took longer to complete their life cycle when reared on *Solanum rigescens* than when reared on *S.hermannii*.

Both *S.hermannii* and *S.rigescens* are common around Grahamstown and support large numbers of *C.tigrina*. Since *S.rigescens* appeared to be suboptimal for beetles collected from *S.hermannii* (Chapter 7), it was possible that beetles found on *S.rigescens* in the field belonged to a separate population that had temporarily adapted to it. Bush (1969) defined such a host-adapted population (host race, biotype) as "a population of a species living on and showing a preference for a host which differs from the host or hosts of other populations of the same species".

Host races of phytophagous insects have been studied among many species attacking cultivated plants (eg. Bush 1969, Hsaio 1978, Tabashnik 1983, Horton *et al.* 1988). Host adaptation can be of major economic importance, since it can enable an insect to exploit a vacant ecological niche previously unavailable to it and colonise a larger area (Thorpe 1930). This can apply to both agriculture and weed control, since the introduction of either crop or weed plants provides vacant ecological niches. Some biotypes of the Colorado potato beetle (*Leptinotarsa decemlineata* (Say)) are serious potato pests in the United States, while others attack native *Solanum* plants (Hsaio 1978, Horton *et al.* 1988). The Cochineal insect (*Dactylopius tomentosus*) comprises biotypes in the United States, two of which have been introduced into Australia to control *Opuntia stricta* Haworth and *Opuntia inermis* De Candolle (see Thorpe 1930). The formation of host races is also of evolutionary interest, since it has been suggested that sympatric speciation may proceed via this route (see Jaenike 1981).

Host adaptation and the formation of host races involves trade-offs in performance across hosts, such that the fitness of a biotype on one host must be negatively correlated with fitness on a second host (Rausher 1984). Host races of *C.tigrina* could thus be demonstrated if beetles collected from either *S.hermannii* or *S.rigescens* displayed greater fitness when reared on the same rather than the alternative host plant. The fitness of beetles from both field populations was evaluated on the two host plants, using three biological indicators. These comprised the mortality of the immature stages, duration of the life cycle and size of the pupae and adults.

## 8.2. Mortality of the immature stages.

The Kruskal-Wallis test demonstrated large differences in total mortality ($p<0,001$) between the four treatments (Fig.8.1).

### *a. Effect of host plant.*

Mann-Whitney comparisons demonstrated that the total mortality of *S.hermannii* larvae fed on *S.rigescens* (HR treatment) was significantly higher ($p<0,005$) than that of *S.hermannii* larvae fed on *S.hermannii* (HH treatment). Similarly the total mortality of *S.rigescens* larvae fed on *S.rigescens* (RR treatment) was significantly higher ($p<0,005$) than that of *S.rigescens* larvae fed on *S.hermannii* (RH treatment). Larvae from both field populations suffered higher mortality when reared on *S.rigescens*.

### *b. Effect of origin of larvae.*

There was no significant difference in total mortality ($p>0,05$) between *S.hermannii* and *S.rigescens* larvae fed on *S.hermannii* (HH and RH treatments). The same trend was shown ($p>0,05$) between *S.hermannii* and *S.rigescens* larvae fed on *S.rigescens* (HR and RR

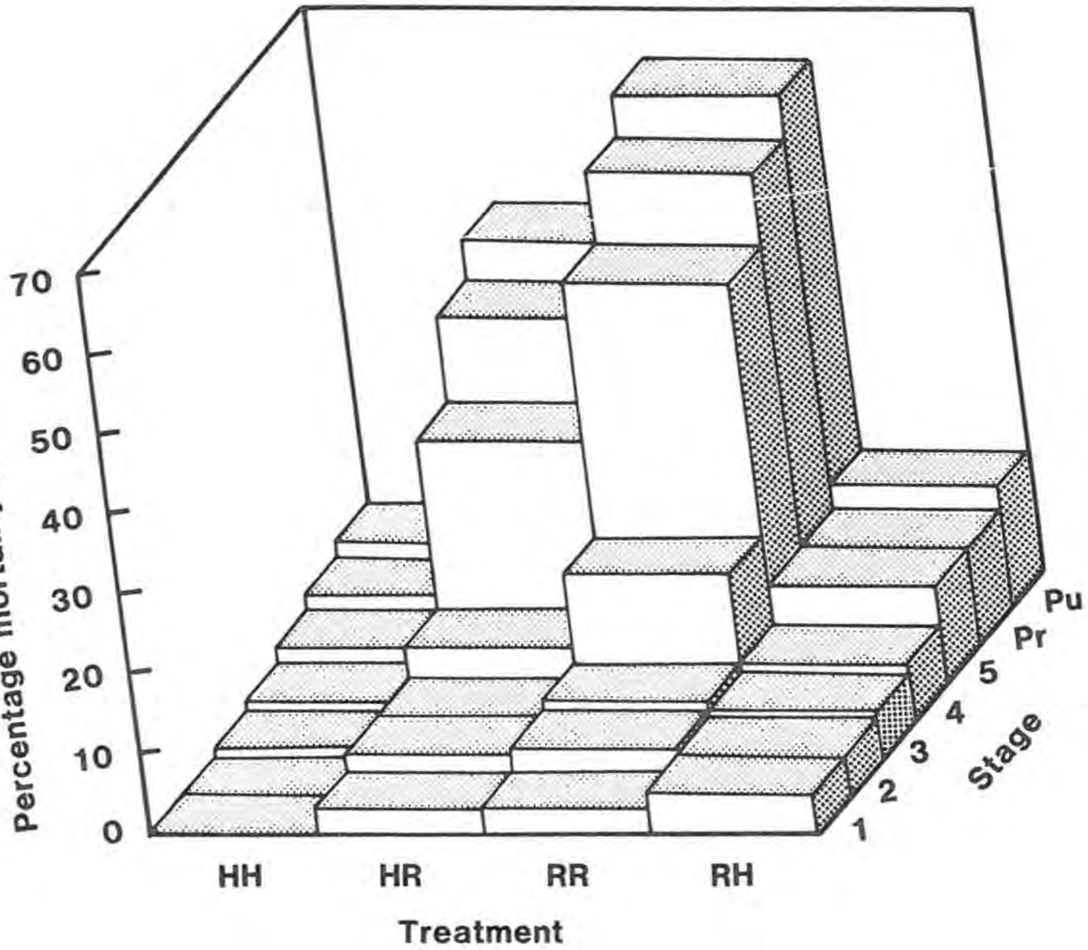

**Fig.8.1.** Three dimensional histogram showing the cumulative percentage mortality during the immature stages of *Conchyloctenia tigrina*. The mortality of the five larval instars (1-5), prepupae (Pr) and pupae (Pu) are represented for each of four treatments. The treatments are keyed according to the host plants on which the beetles originated and the plants on which their larvae were reared. For example HR beetles originated from *Solanum hermannii* and were reared on *Solanum rigescens*.

treatments). This showed that mortality was not influenced by the origin of the larvae.

### *c. Differential mortality of different immature stages.*

The respective mortalities of each immature stage (Fig.8.1) gives an indication of where in the life cycle mortality was most severe. The Kruskal-Wallis test showed significant differences in the fourth and fifth instars and the prepupae ($p<0,05$). Mann-Whitney comparisons of *S.hermannii* larvae fed on both hosts (HH and HR treatments) showed a significant difference ($p<0,005$) in only the fifth instar. Comparisons of the *S.rigescens* larvae fed on both hosts (RH and RR treatments) showed significant differences ($p<0,05$) in the fourth and fifth instars and the prepupae. The late larval instars were expectedly the worst affected, since over 60% of the total food required for insect larval development is usually consumed during the final instar (Hodkinson and Hughes 1982). *S.rigescens* appeared to have no effect on the mortality of pupae.

## **8.3. Duration of the life cycle.**

The Kruskal-Wallis test demonstrated significant differences in the duration of the life cycle ($p<0,001$) between the treatments (Fig.8.2).

### *a. Effect of host plant.*

Mann-Whitney comparisons demonstrated that *S.hermannii* larvae fed on *S.rigescens* (HR treatment) took significantly longer ($p<0,005$) to complete their life cycle than *S.hermannii* larvae fed on *S.hermannii* (HH treatment). Similarly, *S.rigescens* larvae fed on *S.rigescens* (RR treatment) took significantly longer ($p<0,005$) than *S.rigescens* larvae fed on *S.hermannii* (RH treatment). Larvae from both field populations took longer to complete their life cycle when reared on *S.rigescens*.

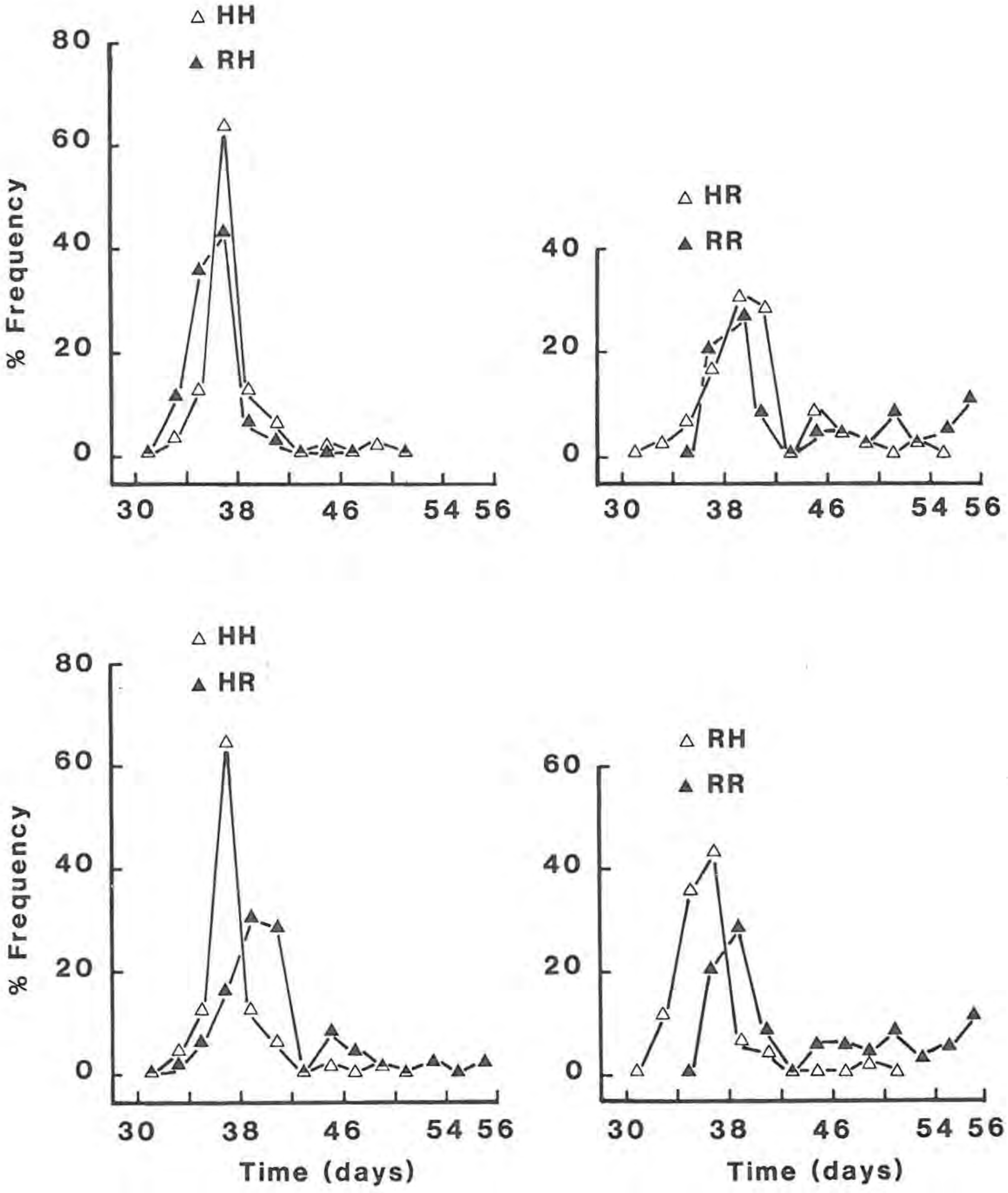

**Fig. 8.2.** Frequency polygons representing the distributions of the total developmental times of the immature stages of *Conchyloctenia tigrina*. Pairwise comparisons are made between beetles of the same origin which are fed different hosts (HH and HR; RH and RR) and between beetles of different origins which are fed the same hosts (HH and RH; RH and RR). H= *Solanum hermannii* and R= *Solanum rigescens*.

### *b. Effect of origin of larvae.*

There was no significant difference in life cycle duration (p>0,05) between *S.hermannii* and *S.rigescens* larvae fed on *S.rigescens* (HR and RR treatments), showing that both populations were equally influenced by *S.rigescens*. However, a significant difference was reflected (p<0,005) between *S.hermannii* and *S.rigescens* larvae fed on *S.hermannii* (HH and RH treatments). This does not, however, suggest host adaptation since beetles from both populations completed their life cycle in a similar time (Mode= 36,6 days for RH cf. 37,0 days for HH in Fig.8.2). Host adaptation would have necessitated a longer life cycle for *S.rigescens* larvae, since they would not have been feeding on their "adapted" host while *S.hermannii* larvae fed *S.hermannii* would have been. The significant difference recorded in the latter comparison may be a manifestation of large sample sizes statistically overemphasizing small differences, since the HH and RH frequency distributions do not appear to be that different in Fig.8.2. In spite of the latter inconsistency, the results do not demonstrate host adaptation in either of the populations.

### *c. Differential rates of development of different immature stages.*

The respective durations of each of the immature stages on *S.rigescens* relative to *S.hermannii* is indicated in Table 8.1. Mann-Whitney comparisons of larvae from both populations reared on the two hosts showed that the second, third, fourth and fifth instars all took significantly longer to develop on *S.rigescens*. The non-feeding prepupae and pupae were generally not affected by host plant, although the prepupae of *S.rigescens* beetles took significantly longer to develop on *S.rigescens*. The differential rates of development differ from the results of larval mortality, where significant differences only became apparent during and after the fourth instar.

Table 8.1. Comparisons of the median durations (days) of the immature stages of *Conchyloctenia tigrina* originating from two different hosts and reared on either of these. SH= *Solanum hermannnii* and SR= *Solanum rigescens*. 1st-5th= first to fifth larval instars, Prep= prepupa.

| Origin | Reared | 1st | 2nd | 3rd | 4th | 5th | Prep | Pupa |
|---|---|---|---|---|---|---|---|---|
| SH | SH | 4,7 | 4,0 | 4,0 | 4,5 | 7,0 | 2,9 | 10,1 |
| SH | SR | 5,0 | 4,3 | 4,5 | 5,2 | 7,7 | 2,9 | 10,2 |
| | | NSK | *** | *** | *** | *** | NS | NSK |
| SH | SH | 4,7 | 4,0 | 4,0 | 4,5 | 7,0 | 2,9 | 10,1 |
| SR | SH | 4,5 | 4,0 | 4,0 | 4,6 | 6,2 | 2,9 | 10,0 |
| | | NSK | * | *** | NS | *** | NS | NSK |
| SH | SR | 5,0 | 4,3 | 4,5 | 5,2 | 7,7 | 2,9 | 10,2 |
| SR | SR | 5,0 | 4,3 | 4,2 | 5,0 | 7,3 | 3,0 | 10,0 |
| | | NSK | NS | NS | NS | NS | NS | NSK |
| SR | SH | 4,5 | 4,0 | 4,0 | 4,6 | 6,2 | 2,9 | 10,0 |
| SR | SR | 5,0 | 4,3 | 4,2 | 5,0 | 7,3 | 3,0 | 10,0 |
| | | NSK | *** | *** | *** | *** | ** | NSK |

NSK= Intergroup differences not significant at 0,05 level by Kruskal-Wallis test: pairwise comparisons not conducted.
*=p<0,05; **=p<0,01; ***=p<0,005: using Mann-Whitney test.

## 8.4. Pupal and adult size.

The Kruskal-Wallis test showed significant differences in pupal mass and adult length ($p<0,005$) between the treatments. The trend was consistent for both sexes. Pupal mass differences are indicated in Fig.8.3; adult length was strongly correlated with pupal mass ($r=0,91$) and showed virtually identical trends.

### *a. Effect of host plant.*

Mann-Whitney comparisons showed that male and female pupae of *S.hermannii* larvae weighed significantly more ($p<0,005$; $p<0,005$ respectively) when reared on *S.hermannii* than on *S.rigescens*. They were also significantly longer ($p<0,01$; $p<0,005$ respectively) when reared on *S.hermannii*. Similarly male and female pupae of

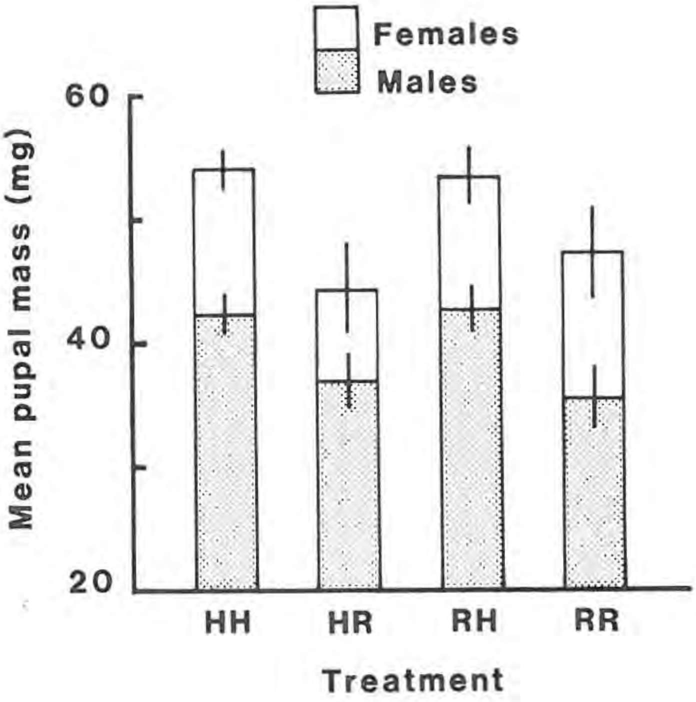

**Fig.8.3.** Mean pupal masses of female and male *Conchyloctenia tigrina*. The histograms are keyed according to the origin of the beetles and the host plant on which reared. HR beetles, for example, originated from *Solanum hermannii* and were fed on *Solanum rigescens*. The vertical bars represent two standard errors of the means.

*S.rigescens* larvae weighed significantly more ($p<0,005$; $p<0,005$ respectively) when reared on *S.hermannii* than on *S.rigescens*. They were also significantly longer ($p<0,05$; $p<0,005$ respectively) when reared on *S.hermannii*. Larvae from both field populations attained a smaller size when reared on *S.rigescens*.

### *b. Effect of origin of larvae.*

There were no significant differences ($p>0,05$) in pupal mass and adult length between either *S.hermannii* and *S.rigescens* beetles reared on *S.hermannii* or on *S.rigescens*. This showed that size was not influenced by the origin of the beetles.

## 8.5. Feeding and oviposition preferences.

The relative amounts of *S.hermannii* and *S.rigescens* eaten by 125 beetles, comprising 25 replicates, of each population are represented in Fig.8.4a. Similarly the number of egg cases deposited on the two plants, by 15 females from each population, is shown in Fig.8.4b. Since there was no significant difference between previous results (mortality etc.) for the two populations of beetles and since the experiments reported above showed no significant differences ($p>0,05$) between the populations, the amounts eaten and egg cases oviposited by beetles originating from the two plant species were combined to test for host plant preference. The beetles showed no preference ($p>0,05$) for either host plant either as food or for oviposition. The two plants thus appear to be equally acceptable. This does not appear to be a laboratory artifact since adults and larvae of *C.tigrina* are commonly seen on *S.rigescens* in the field. Experimental leaves were obtained in both cases from areas where *C.tigrina* was active.

## 8.6. Discussion.

The populations of beetles, collected in the field from each of *S.hermannii* and *S.rigescens*, were assumed to be samples from the same population since no evidence of host races was obtained. A

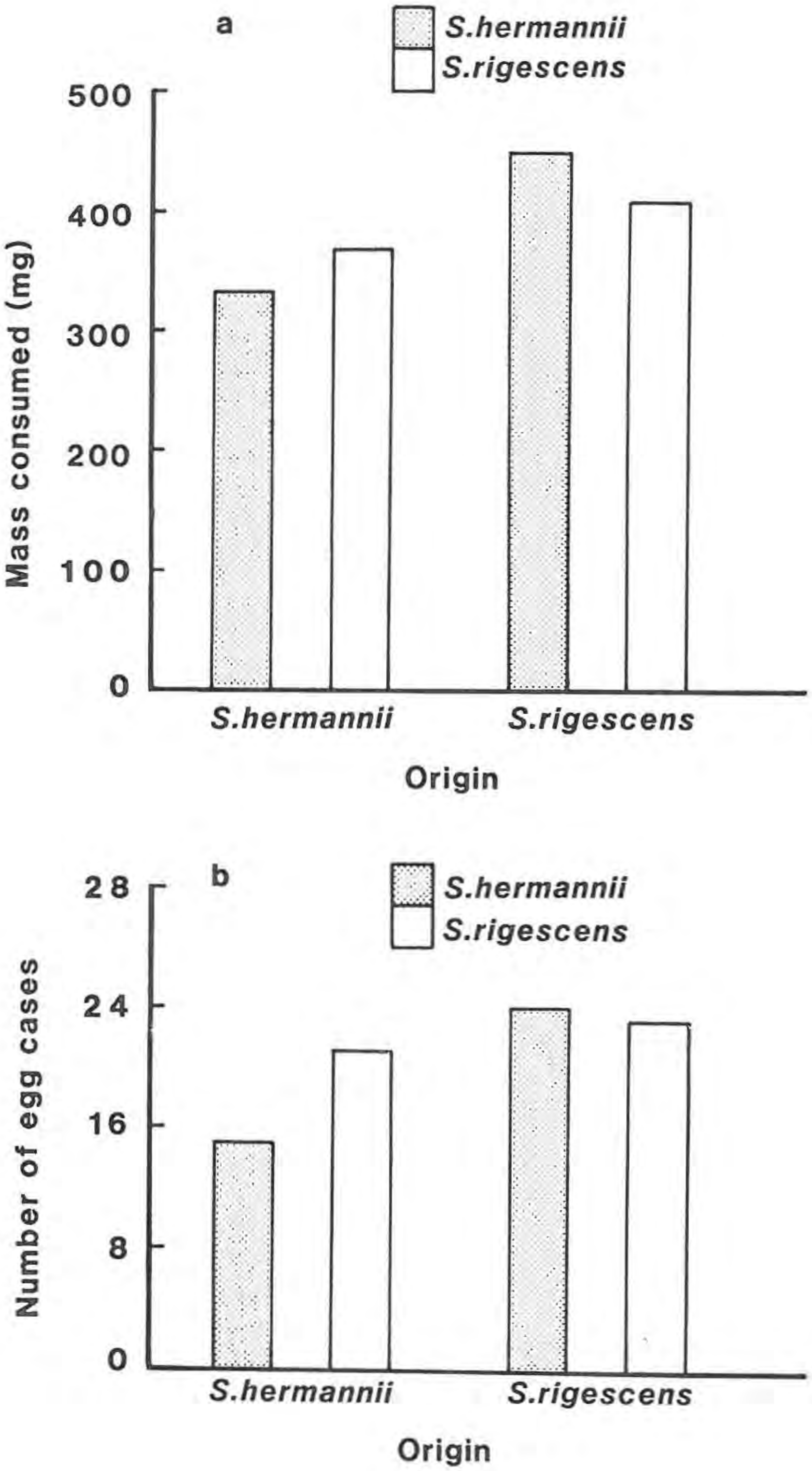

**Fig.8.4.** a. Total amount of leaf tissue of *Solanum hermannii* and *Solanum rigescens* consumed by 125 beetles (25 replicates) originating from each host. b. Total number of egg cases deposited on *Solanum hermannii* and *Solanum rigescens* by 15 females originating from each host.

similar study of the tortoise beetle, *Deloyala guttata*, in the U.S.A., also produced no evidence of trade-offs in performance on different *Ipomea* hosts (Rausher 1984). *S.rigescens* was found to be an inferior host relative to *S.hermannii* irrespective of beetle origin, confirming earlier experiments in Chapter 7. The harmful effects of *S.rigescens* were manifested mainly during the immature stages of *C.tigrina*, and were indicated by increased larval mortality, longer developmental times and, eventually, smaller adult size.

In view of the relative unsuitabilty of *S.rigescens* as host, the willingness of *C.tigrina* to feed and oviposit on *S.rigescens* in both the field and the laboratory is difficult to explain. A possible explanation is that *S.hermannii* may be the original host and *S.rigescens* an addition to the host range. *S.rigescens* may share chemical or other characteristics with *S.hermannii* which make it acceptable to *C.tigrina*, but may also have harmful characteristics which make it a poor host. An alternative might be that *S.rigescens* is in the process of aquiring chemical defences against *C.tigrina*, and may thus be one step ahead of *S.hermannii* in the classic co-evolutionary pattern. In either event, some beetles can be regarded as "trapped" on a suboptimal host, by virtue possibly of a similarity in chemical attractants. Selection of suboptimal hosts is, however, not uncommon in nature. A review by Thompson (1988) indicated many cases where oviposition preferences were correlated with poor performances (growth, survival and fecundity) of offspring. The results are thus consistent with the view that insects do not necessarily select the best possible hosts.

Relationships between insects and plants revolve mainly around host selection by the insect and plant resistance to the insect, these factors being closely connected (Beck 1965). This author defined resistance as the total hereditary characteristics whereby a plant reduces its utilization as a host by an insect. Painter (1958) recognised two resistance mechanisms encompassed by this definition. Non-preference affected insect behaviour via host selection or acceptence, while antibiosis adversely affected insect growth and survival. The apparent resistance of *S.rigescens* to *C.tigrina* is not due to the non-preference effect, since the plant was acceptable to the beetles for both food and oviposition during choice tests. Antibiotic effects were, however, reflected by increased larval mortality, longer development and smaller size. The effects of larval mortality are obvious while smaller adult size may imply reduced fecundity, as fecundity in insects is often correlated with size (Englemann 1970). Slower larval development is also effective as it could greatly increase exposure to abiotic mortality factors, predation and parsitism (Brown *et al.* 1980). Schultz (1988) mentioned that the effectiveness of many parasitoid species depends on larval growth rates and that parasitism increases when larval growth rate is slowed. The harmful effects of *S.rigescens* may, however, be a result of nutrient characteristics and not necessarily chemical defences, or it may be a combination of the two.

# 9. HERBIVORE GUILDS, HOST RANGES AND DIVERSITY RELATIVE TO OTHER PLANT TAXA

## 9.1. Introduction.

The herbivore communities of *S.mauritianum* and five indigenous *Solanum* species have been described and compared (Chapters 3 and 5). This chapter firstly reviews aspects of *Solanum* herbivory and considers the following. 1. The structure of the herbivore guilds on different plant species, in particular the proportions of endophagous herbivores. 2. The extent of the host ranges of the most common *Solanum* herbivores.

The next topic concerns the diversity of herbivores on *Solanum* species. The diversity of insect herbivores on plants may be determined by numerous interrelated factors (reviewed by Strong *et al.* 1984 and Zwölfer 1986). These include the morphological complexity, size, geographic range, evolutionary history and taxonomic isolation of the plant as well as the diversity of the habitats in which it occurs. The relative influences of these factors on the herbivore diversity of *Solanum* species are not discussed, since the surveys mainly involved opportunistic sampling of the most common plants and were not designed to test any of these parameters.

The apparent paucity of insects on species of Solanaceae has been attributed to the fact that these plants are morphologically and chemically well defended (Drummond 1986) and thus relatively immune to insect attack (Hsiao 1986). The diversity of herbivores on *Solanum* plants are examined relative to other plant taxa to determine whether *Solanum* faunas are indeed relatively depauperate. These comparisons include the following. 1. An evaluation of the herbivore fauna of *S.mauritianum* in South Africa relative to weed species introduced to the U.S.A. These include plants from the families Asteraceae, Chenopodiaceae, Cruciferae, Leguminaceae and Umbelliferae. 2. An evaluation of the herbivore faunas of indigenous *Solanum* species in South Africa relative to plant taxa indigenous to Europe and the U.S.A. Most of the plants are of the family Asteraceae, due to the apparent lack of comparative studies on Solanaceae.

## 9.2. Guild structure (niche classification) of *Solanum* herbivores.

The structure of the herbivore guilds associated with the *Solanum* species most comprehensively studied in South Africa is shown in Fig.9.1b-g. The situation in the different species appeared to be similar to that reflected by the overall picture in Fig.9.1a. The proportions of ectophages relative to endophages showed no significant differences between the plants ($Chi^2_{[5]}$= 0,58: p>0,05). Similarly, the proportions of chewers relative to sap suckers showed no significant differences between the plants ($Chi^2_{[5]}$= 4,78: p>0,05). The overall picture on *Solanum* species reflected a predominance of ectophagous (73%) relative to endophagous (27%) herbivores. Ectophagous species, in which Coleoptera and Hemiptera dominated, comprised roughly equivalent proportions of chewers (39%) and sap suckers (34%). The endophages comprised mainly borers (10%) and saprophages (10%), with some gall-formers (6%) and miners (1%). The borers were mainly Lepidoptera and Diptera which attacked fruit and flowers. The seven saprophages, which comprised Diptera infesting insect-damaged fruit, were treated as herbivores as they fed on living and decaying tissue. The gall formers comprised Lepidoptera and Diptera, while a single dipteran leaf miner was encountered.

Examination of the endophagous guild structure revealed some notable features. The saprophage component, representing dipteran borers, associated with caterpillar-damaged fruit, was represented on all plants except *S.coccineum* and *S.rigescens*, although caterpillars occurred in fruit of the latter species. This correlates with the presence of small berries on these two species relative to the much larger fruit of the other plants. Size may thus limit the diversity of fruit-associated herbivores in these two plants, as the berries are presumably too small to harbour secondary infestations by these

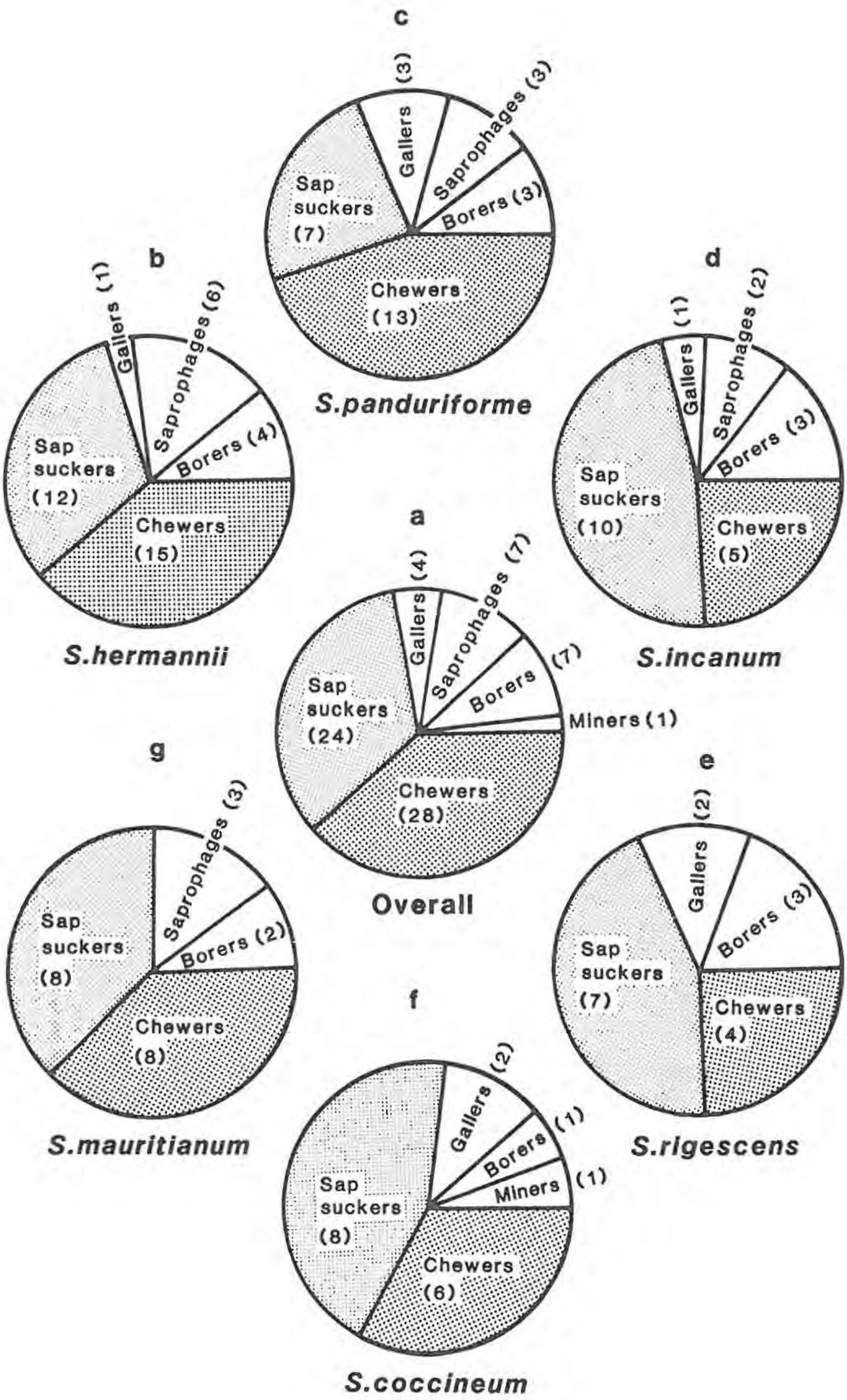

**Fig.9.1.** Structure of the insect herbivore guilds associated with *Solanum* species. Shaded sectors represent ectophagous herbivores and unshaded sectors indicate endophages. Numbers in parentheses indicate numbers of species in each guild.

flies. Gall-forming insects were represented on all plant species except *S.mauritianum*, a situation not surprising on introduced plants. Miners were virtually absent and occurred only on *S.coccineum*, where a single species of Agromyzidae was occasionally encountered. Borers were represented on all plants and comprised species attacking reproductive tissues. No stem borers were detected, except possibly larvae of a buprestid encountered on foliage, indicating a vast un- or under-utilized resource on *Solanum* species.

## 9.3. Host ranges of *Solanum* herbivores.

The host ranges of the 25 most common herbivores on the species of *Solanum* examined is shown in Table 9.1. Three of the nine plant species were examined on only a few occasions and could thus only confirm presence, but not absence of particular herbivores. The occurrence of these herbivores (in at least 20% of samples taken) on the six most comprehensively sampled plant species is indicated in Fig.9.2. None of these species was common on *S.mauritianum*, confirming its position at the lower end of the diversity spectrum. On *S.panduriforme*, 48% of the herbivores were common compared with 40% on *S.incanum*. On both *S.rigescens* and *S.hermannii*, 32% of the herbivores were common, supporting the suggestion (Chapter 5) that temperate *Solanum* species are less diverse than subtropical species, at least for the commonly-occurring species.

The breadths of the host ranges of these common herbivores were evaluated by their presence on the five best sampled indigenous plants (Fig.9.3). Most of the herbivores (68%) occurred on three or more hosts, displaying a tendency towards oligophagy. Only two possibly monophagous species were recorded, namely the cecidomyiid and lonchaeid gall-formers of *S.panduriforme* leaves. The buprestid, which only occurred on one of the five hosts used in Fig.9.3, was also collected from *S.tomentosum* (Table 9.1). The most polyphagous of the herbivores, occurring on all five of the plants in Fig.9.3, were the flea beetle (*Chaetocnema* sp.), tip wilter (*Acanthocoris* sp.) and gall-forming gelechiid (*S.* sp.nr. *concreta*). Furthermore, the flea beetles also occurred on *S.acanthoideum* and *S.tomentosum*, while the gelechiids were also found on *S.tomentosum* (Table 9.1).

Table 9.1. Host ranges, amongst *Solanum* plants sampled, of the most common herbivores of *Solanum* species in South Africa (those found in at least 20% of the samples of at least one host).

| HERBIVORES | PLANTS SAMPLED | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Comprehensive | | | | | | Limited | | |
| | Co | He | In | Ma | Pa | Ri | Ac | Am | To |
| **Fruit** | | | | | | | | | |
| *D.laisalis* | - | + | + | - | + | - | + | + | |
| Gelechiidae (AcRh 572) | + | - | - | - | - | + | | | + |
| *S.ophyroides* | - | + | - | - | + | - | + | | |
| Agromyzidae (AcRh 467) | - | + | + | - | + | - | + | | |
| *Atherigona* sp. | - | + | + | - | + | - | | | |
| **Flowers** | | | | | | | | | |
| *S.* sp.nr. *concreta* | + | + | + | - | + | + | | | + |
| *Pria* sp. | - | + | + | + | + | + | | | |
| **Foliage** | | | | | | | | | |
| *Chaetocnema* sp. | + | + | + | + | + | + | | + | + |
| *C.tigrina* | + | + | - | - | + | + | | | |
| *C.hybrida* | - | + | + | - | + | - | | + | |
| *H.hirta* | + | + | - | + | - | + | + | | + |
| *E.canina* | - | + | + | - | + | - | | | |
| *E.paykulli* | + | + | - | - | + | - | | + | |
| Buprestidae (AcRh 540) | - | - | - | - | + | - | | | + |
| *Acanthocoris* sp. | + | + | + | + | + | + | | | |
| Cicadellidae (AcRh 530) | + | - | + | + | + | - | | | + |
| *D.apicalis* | + | + | + | + | - | + | | | + |
| Membracidae (AcRh 484) | + | + | - | - | - | + | | | + |
| *Spilostethus* sp. | + | + | + | + | + | - | + | | + |
| *U.hystricellus* | + | - | + | - | + | - | | | + |
| Gelechiidae (AcRh 480) | + | - | - | - | - | + | | | + |
| Lepidoptera (AcRh 512) | + | - | - | - | + | - | | | |
| *P.* sp.nr. *diversipennis* | + | - | - | - | + | - | | | |
| Cecidomyiidae (AcRh 609) | - | - | - | - | + | - | | | |
| Lonchaeidae (AcRh 610) | - | - | - | - | + | - | | | |

+ Indicates presence on more than one occasion.
- Indicates absence in samples.
Co= *S.coccineum*, He= *S.hermannii*, In= *S.incanum*, Ma= *S.mauritianum*, Pa= *S.panduriforme*, Ri= *S.rigescens*, Ac= *S.aculeatissimum*, Am= *S.acanthoideum*, To= *S.tomentosum*.

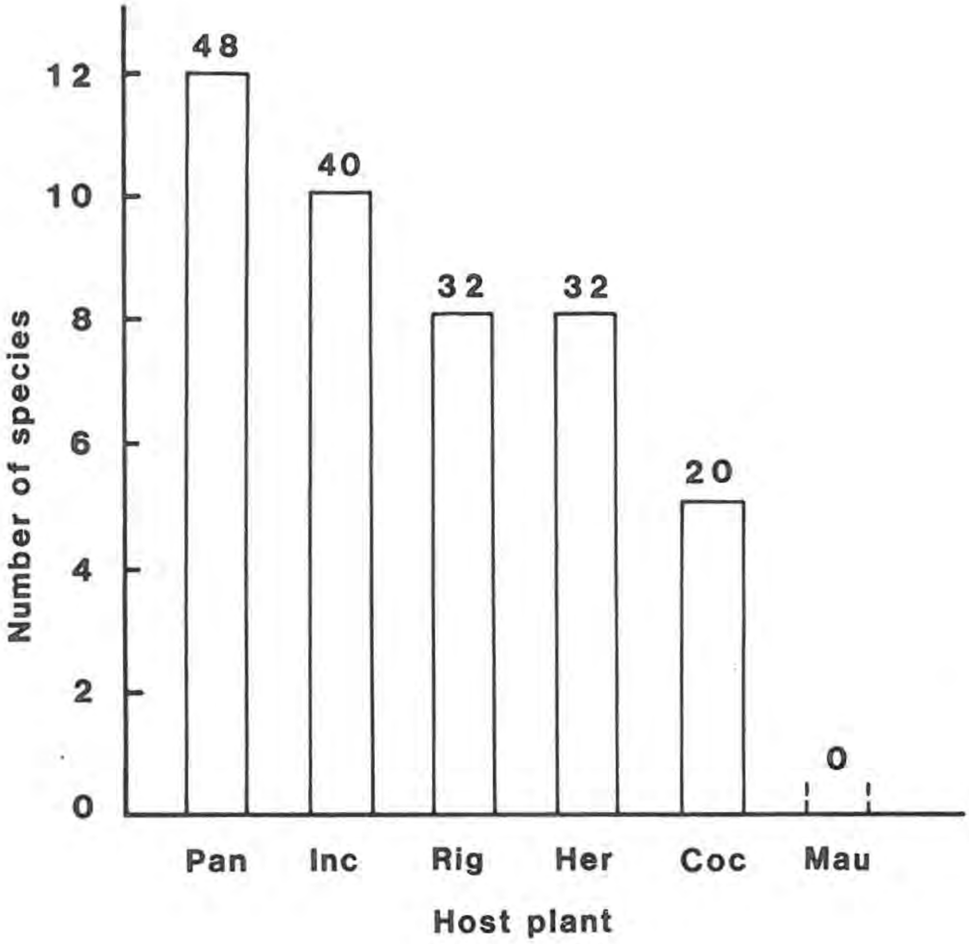

**Fig.9.2.** Occurrence of the 25 most common *Solanum* herbivores on each of six host plants, in at least 20% of samples taken from each plant. Numbers on the bars indicate the percentages of these herbivores that occurred on each host plant. Pan= *Solanum panduriforme*, Inc= *Solanum incanum*, Rig= *Solanum rigescens*, Her= *Solanum hermannii*, Coc= *Solanum coccineum* and Mau= *Solanum mauritianum*.

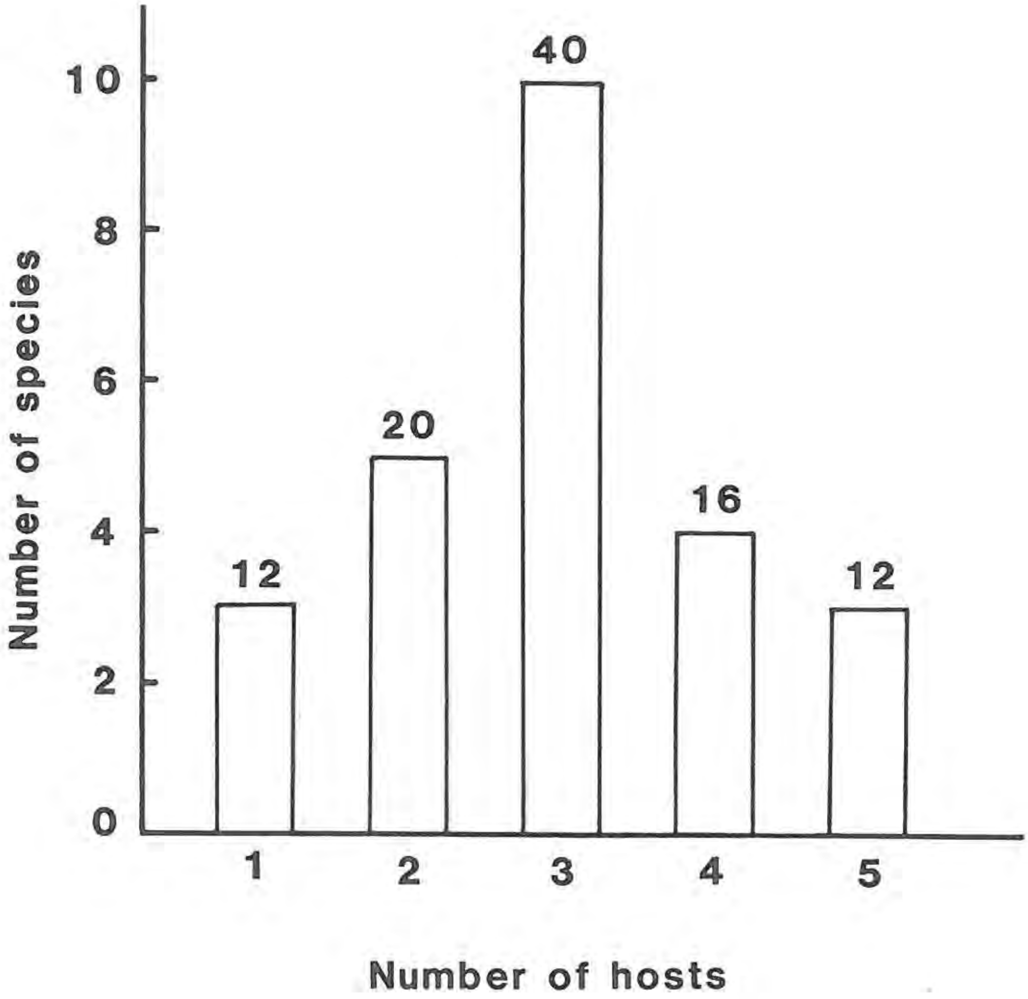

**Fig.9.3.** Occurrence of the 25 most common *Solanum* herbivores on five indigenous hosts. Numbers on the bars indicate the percentage of the herbivores feeding on different combinations of hosts.

## 9.4. Comparison of the fauna of *Solanum* species with that of other plant taxa.

The herbivore diversity of *S.mauritianum* in South Africa and of other exotic herbaceous weeds in the U.S.A. is represented in Table 9.2. Similarly, the diversities of the five indigenous *Solanum* species surveyed in South Africa are compared to those of other

Table 9.2. Numbers of herbivore species on *Solanum mauritianum* in South Africa and various exotic herbaceous weeds in the U.S.A.

| TAXA | NUMBERS |  | REFERENCE |
|---|---|---|---|
|  | Total | Common |  |
| **Asteraceae** |  |  |  |
| *Silybum marianum*<br>(Milk thistle) | 48 | 19 | Goeden (1971b) |
| *Carduus pycnocephalus*<br>(Italian thistle) | >40 | 7 | Goeden (1974) |
| *Cirsium vulgare*<br>(Bull thistle) | 30 | 4 | Goeden & Ricker (1986a) |
| *Xanthium spinosum*<br>(Spiny clotbur) | 21 | 9 | Hilgendorf & Goeden (1983) |
| *Xanthium strumarium*<br>(Cocklebur) | 60 | 40 | Hilgendorf & Goeden (1983) |
| **Chenopodiaceae** |  |  |  |
| *Salsola australis*<br>(Russian thistle) | 91 | 22 | Goeden & Ricker (1968) |
| **Cruciferae** |  |  |  |
| *Barbarea vulgaris*<br>(Winter cress) | 35 | 4 | Root & Tahvanainen (1969) |
| **Leguminaceae** |  |  |  |
| *Coronilla varia*<br>(Crown vetch) | 54 | 33 | Wheeler (1974) |
| **Solanaceae** |  |  |  |
| *Solanum elaeagnifolium*<br>(Silverleaf nightshade) | 22 | 3 | Goeden (1971a) |
| *Solanum mauritianum*<br>(Bugweed) | 21* | 2 |  |
| **Umbelliferae** |  |  |  |
| *Conium maculatum*<br>(Poison hemlock) | 20 | 1 | Goeden & Ricker (1982) |

* Rare and occasional species excluded.

plant taxa indigenous to Europe and the U.S.A. (Table 9.3).

Table 9.3. Numbers of insect herbivore species on indigenous *Solanum* species in South Africa and on some indigenous herbaceous taxa in Europe and the United States.

| TAXA | NUMBERS Total | Common | REFERENCE |
|---|---|---|---|
| **Asteraceae** | | | |
| *Silybum marianum*<br>(Milk thistle: Europe) | >130 | 35 | Goeden (1976) |
| *Carduus pycnocephalus*<br>(Italian thistle: Europe) | 80 | 18 | Goeden (1974) |
| *Cirsium vulgare*<br>(Bull thistle: Europe) | >65 | >40 | Zwölfer (1965) |
| *Cirsium californicum*<br>(Thistle: U.S.) | 59 | 8 | Goeden & Ricker (1986b) |
| *Cirsium proteanum*<br>(Thistle: U.S.) | 31 | 6 | Goeden & Ricker (1986b) |
| *Ambrosia dumosa*<br>(White bur-sage: U.S.) | >89 | 20 | Goeden & Ricker (1976a) |
| *Ambrosia psilostachya*<br>(Western ragweed: U.S.) | >113 | 31 | Goeden & Ricker (1976c) |
| *Ambrosia chenopodiifolia*<br>(San Diego bur-sage: U.S.) | 31 | 5 | Goeden & Ricker (1976b) |
| *Ambrosia eriocentra*<br>(Wooly bur-sage: U.S.) | 33 | 9 | Goeden & Ricker (1976b) |
| *Ambrosia ilicifolia*<br>(Hollyleaf bur-sage: U.S.) | 19 | 6 | Goeden & Ricker (1976b) |
| **Papaveraceae** | | | |
| *Argemone corymbosa*<br>(Prickly poppy: U.S.) | 2 | 2 | Goeden & Ricker (1985) |
| *Argemone munita*<br>(Prickly poppy: U.S.) | 14 | 3 | Goeden & Ricker (1985) |
| **Solanaceae** | | | |
| *Solanum hermannii*<br>(Sodom's apple: S.A.) | 38* | 9 | |
| *Solanum rigescens*<br>(S.A.) | 16* | 8 | |
| *Solanum panduriforme*<br>(Yellow bitter apple: S.A.) | >29* | >12 | |
| *Solanum incanum*<br>(Grey bitter apple: S.A.) | >21* | >8 | |
| *Solanum coccineum*<br>(S.A.) | 18* | 5 | |

* Rare and occasional species excluded.

Comparisons are made between species listed as "common" since rare and occasional herbivores, which were included in the herbivore lists of all the plants surveyed by other workers, were excluded from the list of *Solanum* herbivores. The reason for the exclusion of such occasional generalists was that their numbers are likely to be greatly affected by local insect diversity patterns.

The conclusion of Strong *et al.* (1984), that most introduced plants are able to acquire fair numbers of herbivorous species, is affirmed by Table 9.2. Weeds with particularly rich faunas include cocklebur (Hilgendorf and Goeden 1983), crown vetch (Wheeler 1974) and Russian thistle (Goeden and Ricker 1968). However, some weeds have poor faunas. Of the 11 plants compared, the two *Solanum* species, *S.mauritianum* and *S.elaeagnifolium*, reflected the second and third lowest diversity respectively of herbivores. The fauna of *S.elaeagnifolium* in southern California (Goeden 1971a) was similar to that of *S.mauritianum* in South Africa. The position of *S.mauritianum*, in particular, at the lower end of this diversity spectrum is notable, considering that it constitutes a large shrub or small tree (Symon 1981) while the remaining species are herbaceous. Strong *et al.* (1984) and Zwölfer (1986) documented a general trend of increased herbivore diversity from herbs to shrubs to trees.

Similarly, in comparing indigenous taxa, one might expect the herbivore diversity of *Solanum* shrubs to, at least, approach that of the herbs supporting the greatest diversity of herbivores. This was not the case as the *Solanum* faunas were positioned somewhere between the lower and mid ranges of the herb diversity spectrum (Table 9.3).

## 9.5. Discussion.

The feeding guilds of *Solanum* herbivores are characterized by a low incidence of endophagous species and a virtual absence of monophages. This was expected for *S.mauritianum* in South Africa, since these features characterize the faunas of introduced plants (Strong *et al.* 1984, Goeden and Ricker 1986a). Endophagy and narrow host ranges are generally considered to be features of more specialized herbivores, and colonization of plants by these normally takes much longer than it does for less specialized herbivores (Strong *et al.* 1984). The endophagous components of the faunas of *S.mauritianum* and the other indigenous species were, however, not significantly different between the six plants, suggesting that a low incidence of endophagy (27%) may be characteristic of *Solanum* plants in South Africa.

In surveys of native *Cirsium* thistles (Asteraceae) in southern California, Goeden and Ricker (1986b, 1987a,b) found a low proportion of endophages (19%) relative to other thistle genera in Europe (34-43%). These authors did not detect any monophagous herbivores on *Cirsium*, although monophages were represented in the faunas of other asteraceous genera in the region, like *Ambrosia* (Goeden and Ricker 1976a,b) and *Xanthium* (Hilgendorf and Goeden 1983). Goeden and Ricker (1987b) considered the low incidence of endophagy and absence of monophagy to be symptoms of the evolutionary immaturity of *Cirsium* insect-plant relationships in southern California. The fact that indigenous *Solanum* species have an endophage proportion equivalent to that of the exotic *S.mauritianum* may suggest that the genus *Solanum* could be a relatively recent addition to the flora of South Africa. Unfortunately, there are no comparative data on *Solanum* faunas in other parts of the world. A low incidence of endophagy and monophagy may simply be a feature of *Solanum* in general.

The colonization of plants by insect herbivores over time has been expressed by an asymptotic curve, the shape of which has been explained by two hypotheses (Strong *et al.* 1984). The "niche saturation" hypothesis predicts slowing of the colonization rate as a result of increasing scarcity of resources (food and space) and intense competition between herbivores. A consequence is that very few unused resources (vacant niches) should exist in well established plant communities. Vacant niches were, however, a regular feature of all the *Solanum* plants examined. Although the absence of certain types of herbivores (eg. gall-formers) was envisaged for *S.mauritianum*, the absence of stem-associated species on indigenous plants was unexpected. However, previous surveys by Lawton (1982) on bracken fern (*Pteridium aquilinum* (L.) Kuhn) and by Goeden and Ricker (1987b) on *Cirsium* thistles also revealed under-usage or lack of use of host-plant resources. The herbivore fauna of *Solanum* plants in South Africa thus supports the conclusion that unused or under-used resources are characteristic of many native plants. This evidence of vacant niches in herbivore communities thus favours the second hypothesis, that of "pool exhaustion" (Strong *et al.* 1984). This predicts slowing of the colonization rate as a result of an increasing scarcity of suitably preadapted insect colonists in the region. Colonization may be slower in taxa, like Solanaceae, which are well defended against herbivory.

*Solanum* species generally seem to support a lower diversity of herbivorous species than most of the herbaceous plant taxa examined from other families. This was reflected in comparisons between both introduced and indigenous taxa. This may support the statements of Drummond (1986) and Hsiao (1986) that effective defences to herbivory have resulted in a paucity of herbivores on Solanaceae. Poor herbivore faunas have been attributed to noxious characteristics in some plants. Examples from southern California include the introduced poison hemlock (Umbelliferae) which is highly toxic (Goeden and Ricker 1982) and the indigenous prickly poppies (Papaveraceae) which incorporate toxins and sticky latex as defences (Goeden and Ricker 1985). These species are poorly attacked as few potential colonists have been able to overcome their defences. The ultimate reasons for this may be complex and could involve factors like insufficient evolutionary time for adaptation, patchiness of the plant's distribution and taxonomic isolation of the plant. The *Solanum* flora of South Africa may thus involve one or more of these possibilities. A weakness of the above argument is that South African *Solanum* species have been compared with other plant taxa in different parts of the world, where the influence of various factors that might affect diversity could differ vastly. *Solanum* species growing in these areas may have richer faunas than South African species. A lack of comparative data on solanaceous faunas from different parts of the world prevents one from concluding that the defences of Solanaceae definitely restrict the diversity of herbivore faunas.

# 10. DISCUSSION

## 10.1. Status of *S.mauritianum* in South Africa.

The impoverished herbivore fauna of *S.mauritianum* in South Africa is similar to that in Mauritius (Neser 1984), where despite the name of the plant, the species is not indigenous. Few of the common herbivores of indigenous *Solanum* species seemed able to colonize the plant and incorporate it in their host ranges. The ladybird *H.hirta* was the only species (besides occasional polyphages) that inflicted obvious damage. This species, however, occurred in a low proportion of samples and seemed restricted to young plants and regrowth, which displayed less dense layers of leaf trichomes and possibly lower concentrations of secondary compounds. It appears that none of the indigenous herbivores are suitably preadapted to exploit the food niches offered by *S.mauritianum*. This situation differs from that described in thistles by Goeden and Ricker (1986a) in southern California, where a number of native thistle herbivores were able to colonize the introduced bull thistle, *Cirsium vulgare* (Savi) Tenore. Other examples of introduced plants with diverse herbivore faunas were discussed in Chapter 9. The importance of local pools of preadapted herbivores in the establishment of herbivore faunas on introduced plants has been emphasized by, for example Jermy (1988) and Zwölfer (1988).

Strong *et al.* (1984) stated that the rate at which herbivores colonize introduced plants depends on the taxonomic and biochemical relatedness between the introduced and indigenous plants. This is based on related plant species often presenting very similar chemical cues, allowing their inclusion in the host ranges of herbivores more often than for taxonomically unrelated plants. Connor *et al.* (1980) showed that both native and introduced trees which were taxonomically and chemically isolated from other plants had impoverished herbivore faunas relative to plants with sympatric close relatives. This trend has been shown by a number of other studies (reviewed by Zwölfer 1986).

*S.mauritianum* is taxonomically distinct from other indigenous *Solanum* species in South Africa (Table 10.1). The plant is classified under the subgenus *Brevantherum* (D'Arcy 1972), which has no indigenous relatives in Africa (Jaeger and Hepper 1986).

Table 10.1. Taxonomic relatedness of *Solanum* species in southern Africa (arranged according to categories specified by D'Arcy (1972)). **

---

Subgenus *Lyciosolanum* Bitt.
  *Solanum guineense* L.

Subgenus *Brevantherum* (Seithe) D'Arcy
Section *Brevantherum* Seithe
  *SOLANUM MAURITIANUM* SCOP. *
Section *Pseudocapsicum* Bitt.
  *Solanum pseudocapsicum* L. *

Subgenus *Potatoe* (G.Don) D'Arcy
Section *Dulcamara* Dumort.
  *Solanum triflorum* Nutt.
Section *Jasminosolanum* Seithe
  *Solanum jasminoides* Paxt. *
  *Solanum seaforthianum* Andr. *
Section *Petota* Dumort.
  *Solanum tuberosum* L. *

Subgenus *Solanum*
Section *Afrosolanum* Bitt.
  *Solanum terminale* Forssk.
Section *Solanum*
  *Solanum americanum* Mill.
  *Solanum burbankii* Bitt.
  *Solanum chenopodioides* Lam.
  *Solanum gracile* Dun.
  *Solanum nigrum* L. *
  *Solanum nodiflorum* Jacq.
  *Solanum retroflexum* Dun.
  *Solanum villosum* Mill.

Subgenus *Leptostemonum* (Dun.) Bitt.
Section *Acanthophora* Dun.
  *Solanum aculeatissimum* Jacq.
Section *Androceras* (Nutt.) Marzell
  *Solanum rostratum* Dun. *
Section *Cryptocarpum* Dun.
  *Solanum sisymbriifolium* Lam. *
Section *Leprophora* Dun.
  *Solanum elaeagnifolium* Cav. *
Section *Melongena* Dun.

*Solanum acanthoideum* E.Mey.
*Solanum aculeastrum* Dun.
*Solanum delagoense* Dun.
*Solanum hermannii* Dun.
*Solanum incanum* L.
*Solanum melongena* L. *
*Solanum panduriforme* E.Mey.
Section *Oliganthes* (Dun.) Bitt.
*Solanum anguivi* Lam.
*Solanum burchellii* Dun.
*Solanum capense* L.
*Solanum coccineum* Jacq.
*Solanum dasyphyllum* Thonn.
*Solanum didymanthum* Dun.
*Solanum giftbergense* Dun.
*Solanum leucophaeum* Dun.
*Solanum moestum* Dun.
*Solanum rigescens* Jacq.
*Solanum supinum* Dun.
*Solanum tomentosum* L.
*Solanum zanzibarense* Vatke
Section *Torva* Nees
*Solanum ferrugineum* Jacq.
*Solanum giganteum* Jacq.
*Solanum hispidum* Pers. *
*Solanum renschii* Vatke

Uncertain.
*Solanum aggerum* Dun. - Sect. Leiodendra Dun.?
*Solanum catombelense* Peyr.
*Solanum crassifolium* Lam. - Sect. Dulcamara ?
*Solanum damarense* Bitt.
*Solanum dasypus* E.Mey.
*Solanum dinteri* Bitt.
*Solanum duplo-sinuatum* Klotzsch - Sect. Oliganthes ?
*Solanum exasperatum* E.Mey. - Sect. Leiodendra ?
*Solanum geniculatum* E.Mey. - Sect. Leiodendra ?
*Solanum kwebense* N.E. Br.
*Solanum lichtensteinii* Willd. - Sect. Acanthophora ?
*Solanum longipes* Dun. - Sect. Dulcamara ?
*Solanum macowanii* Fourc.
*Solanum monotanthum* Damm.
*Solanum multiglandulosum* Bitt.
*Solanum namaquense* Damm.
*Solanum rigescentoides*
*Solanum rogersii* Moore
*Solanum sodomaeodes* Kuntze - Sect. Melongena ?
*Solanum urosepalum* Damm.
*Solanum wrightii* Benth. *

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* Introduced species.
** Species allocated according to classifications by Dunal (1852) and later by D'Arcy (1972) and Jaeger & Hepper (1986).

The *Brevantherum* group, which are characterized by woody thornless species with entire leaves, compound inflorescences borne above the foliage and stellate pubescence (Roe 1967, 1972), appear morphologically (and probably chemically) different from the indigenous South African flora. Species richness patterns of herbivorous insects on introduced plants are said to be determined largely independently of time (Zwölfer 1986, Jermy 1988), after an initial colonization period of between 100 to 300 years (Strong *et al.* 1977, Strong and Levin 1979). Conner *et al.* (1980) confirmed this by showing that taxonomically isolated trees appeared to remain depauperate regardless of their antiquity in a particular region. This implies that the question of whether *S.mauritianum* was introduced to South Africa in the 16th or 19th century is not critical in explaining its depauperacy. Colonists on such plants tend to represent species harbouring already preadapted genotypes, which become exhausted relatively quickly (Jermy 1988). The plant has been present for at least 125 years (Chapter 1) and lack of close relatives would suggest that the asymptote of the herbivore colonization curve has been reached.

Although taxonomic isolation may have had a negative influence on insect herbivore utilization of *S.mauritianum*, it has not reduced the attractiveness of the ripening fruits. These are produced in large numbers and are consumed by several species of frugivorous birds in South Africa (Chapter 3). A parallel situation occurs in Australia, where the rapid spread of the plant has been attributed to frugivorous birds and bats (Symon 1979, Van Dyck 1979). In South Africa, the plant is also an alternative host for the Natal fruit fly, an important economic pest. In Australia, *S.mauritianum* fruit are attacked to a large extent by the fruit fly, *Dacus cacuminatus* (Hering) (Drew and Hooper 1983). Drew (1988) found that fly-infested fruit contained higher protein levels than uninfested fruit, and that more fruit were eaten by the brown pigeon (*Macropygia phasianella* (Temminck)) during the periods when fruit infestation was highest. This may suggest that fly infestations are promoting seed dispersal by the pigeons. It is thus possible that infestation by the Natal fruit fly may also enhance seed dispersal in areas, like Natal, where infestations are high and where Rameron pigeons are major frugivores.

## 10.2. Status of indigenous *Solanum* flora.

Differences in herbivore diversity were observed between the indigenous species examined. Two trends were observed.

1. Species growing in subtropical regions reflected a greater diversity than those growing in temperate regions (Chapter 5). However, *S.panduriforme* and *S.incanum* occur only in subtropical areas and are thus not directly comparable to the temperate species examined. Similarly *S.hermannii*, which was abundant in temperate regions, was too rare in the tropical areas sampled to provide a direct comparison between the two regions. The differences in diversity might thus be related to characteristics of the plants themselves and not to geographic factors.

2. Species that were uncommon in a particular area reflected a poorer herbivore fauna than locally abundant species. This effect of local abundance (Strong *et al.* 1984, Ricklefs 1987) seemed to be manifested by *S.coccineum* around Grahamstown (Chapter 3) and by *S.hermannii* in Natal (Chapter 5). Goeden and Ricker (1987a) showed that some localised species of southern Californian thistles supported poor herbivore faunas and functioned mainly as alternative hosts for polyphagous and oligophagous insects. However, since *S.coccineum* was not sampled in areas where it is common, the possibility exists that a low herbivore diversity is characteristic of the species and not necessarily a reflection of the local abundance effect.

Although the indigenous flora generally support a fair diversity of herbivores, including some oligophagous species which inflict noticeable damage, 15 indigenous plants are listed as problem species (Wells *et al.* 1986). These include the five species examined in this study, *S.coccineum*, *S.hermannii*, *S.incanum*, *S.panduriforme* and *S.rigescens*, some of which reflected diverse faunas. This could suggest that insect herbivory may not be the only factor influencing the distribution and density of these species. Interspecific competition from other plants may be important, due to the nature of many *Solanum* plants. *Solanum* species comprise mainly pioneer plants, which are rarely components of climax vegetation (Symon 1981), and often inhabit disturbed sites where reduced competition would be expected.

The herbivore fauna of *S.hermannii* was the most diverse relative to other indigenous species in the eastern Cape (Chapter 3), suggesting that the plant is indigenous to the Cape and not exotic as suggested by Hepper (1978) and Wells *et al*. (1986). Laboratory experiments on the oligophagous tortoise beetle (*C.tigrina*) support this view, since the beetles displayed greater fitness on *S.hermannii* than any of the other indigenous hosts tested (Chapters 7 and 8). Jaeger and Hepper (1986) also stated that *S.hermannii* was more likely to be South African in origin.

The faunas of the indigenous *Solanum* species studied displayed a few notable features (Chapter 9).

1. A paucity of stem-associated herbivores revealed a vast unexploited food niche. Under-utilization of available resources has also been recorded for bracken (Lawton 1982) and thistle (Goeden and Ricker 1987b) insect faunas. The *Solanum* fauna thus supports the conclusion that herbivorous insect communities are not saturated with species and that unused or under-used resources are a common feature of indigenous plants.

2. The low incidence of endophagous herbivores and virtual absence of monophagous species was similar to the situation on the exotic *S.mauritianum*. Goeden and Ricker (1987b) regarded these features, in part, to signify the evolutionary immaturity of thistle insect-plant relationships in southern California. The

similarity in the endophagous and monophagous proportions of the herbivore faunas of *S.mauritianum* and indigenous *Solanum* species may suggest that the genus *Solanum* could be a relatively recent addition to the flora of South Africa. Alternatively, a low incidence of endophagy and monophagy may be a feature of the genus *Solanum* in general. Faunistic studies of *Solanum* species from other parts of the world are needed to provide the answer.

3. The herbivore diversity of *Solanum* species was generally lower than that of other plant taxa from other parts of the world. This was reflected in comparisons between both introduced and indigenous taxa. Poor herbivore faunas have been correlated with noxious characteristics in some plant taxa (Goeden and Ricker 1982, 1985). This may support the statements of Drummond (1986) and Hsiao (1986) that effective defences to herbivory have resulted in a relative paucity of herbivores on Solanaceae.

## 10.3. Mechanisms of plant resistance.

The Solanaceae are renowned for their effective defences to herbivory, which include both mechanical (spines and trichomes) and chemical defences (Hsiao 1986). As a result, Solanaceae are said to be relatively immune to insect attack (Drummond 1986, Hsiao 1986).

*Solanum* species are characterised by a variety of trichomes on the leaves. These have been taxonomically reviewed (Seithe 1979) in attempts to illustrate phylogenetic trends in the genus. The role of trichomes as a defence against insect herbivory was reviewed by Levin (1973), who illustrated various negative influences on herbivory. These include the trapping or poisoning of insects and the prevention of contact with the plant epidermis. The trichomes of *S.mauritianum* may contribute to its depauperate fauna, since their density on the leaves seems to far exceed that of any of the South African flora. The dense and complex leaf pubescence seems to be characteristic of the subgenus *Brevantherum* (see Roe 1967, 1972), which is not represented in the indigenous flora of Africa (Jaeger and Hepper 1986). The trichomes of the indigenous *Solanum* flora in South Africa, although more sparse, may present a barrier to many herbivorous insects, although, some of the more common *Solanum* folivores are able to cope with this defence.

Both adults and larvae of the tortoise beetle (*C.tigrina*) and ladybird (*H.hirta*) and caterpillars of the noctuid (*P.* sp.nr. *diversipennis*) clear areas on the leaf of trichomes before feeding. The trichome layer of *S.mauritianum* may be too dense for indigenous *Solanum* folivores, requiring too much energy expenditure for clearing. This was suggested by the survival tests discussed in Chapter 7. Larvae of *C.tigrina* only survived until the second instar on *S.mauritianum* leaves, where only very small areas were cleared of trichomes, suggesting that starvation may have been a major cause of mortality. High larval mortality on the indigenous *S.coccineum* may also be related to a higher trichome density relative to other indigenous species tested.

Another defence of Solanaceae incorporates a variety of biochemicals, of which the alkaloids are the most prominent (Hsiao 1986). The steroidal alkaloids, which are common throughout *Solanum* as glycosides (Schreiber 1979), exhibit inhibitory or toxic action against organisms from all major taxonomic groups (Roddick 1979, 1986). Compounds like demissine, leptines and tomatine are highly inhibitory to the feeding and growth of *Leptinotarsa* beetles (Hsiao 1974). *S.mauritianum* contains solasodine glycosides (solasonine, solamargine) which are highly toxic (Van Dyck 1979). The toxic action of glycoalkaloids appears to operate via the impairment of nerve and muscle cell membranes (Roddick 1986). However, they may also impede insect development by interfering with the absorption of dietery sterols required for ecdysone (moulting hormone) synthesis and/or blocking ecdysone synthesis itself (Harborne 1986, Roddick 1986). Glycoalkaloids occur in the soluble phase in plant tissue and can thus be easily mobilised for defence (Roddick 1979).

Although the chemical components of most South African *Solanum* species appear not to have been assayed, it may be that these differ structurally from those of *S.mauritianum*. Harborne (1986) mentioned that slight changes or differences between similar alkaloid molecules can greatly influence their deterrent value. Insects are generally not able to cope with phytochemicals which deviate, albeit slightly, from those within their host range. The inability to cope could be based on toxic deterrence or failure to recognise a plant as a potential host.

The relative contribution of trichomes and phytochemicals to the unpalatability of *Solanum* species has not been investigated. Both factors may act in combination, with volatile chemicals providing an outer line of defence by advertising the presence of noxious characteristics, namely trichomes and toxins. *S.mauritianum* appears to repel most insects, since very few were observed on the plants in the field. Tortoise beetles also avoided leaves of the plant in the laboratory. The resistance of *S.mauritianum* thus seems to be based on the non-preference mechanism (Painter 1958), although an antibiotic mechanism (Painter 1958) causes high mortality if the repellent compounds are ignored. *S.mauritianum* repellency seems, however, to vary between different plants in the field and possibly on seasonal basis. Young plants and regrowth, with apparently fewer leaf trichomes and possibly lower chemical concentrations, were attacked by the ladybird *H.hirta*. However, the status of these "friendly" plants was transitory, as they were not attacked in the following season (Hulley *et al.* in prep.).

A degree of resistance to *C.tigrina* was also observed in two indigenous species, *S.coccineum* and *S.rigescens*. The immature stages of *C.tigrina* suffered higher mortality and took longer to complete their life cycle when reared on either of these species, relative to *S.hermannii* (Chapter 7). The harmful effects of these two species were, however, far less dramatic than those of the exotic *S.mauritianum* and *S.elaeagnifolium*. The partial resistance of *S.coccineum* and *S.rigescens* to tortoise beetles seems to be enforced by an antibiotic mechanism (Painter 1958), since the beetles feed readily on both plants, both in the field and laboratory. The unsuitability of *S.coccineum* for *C.tigrina* may be based, at least in part, on a dense trichome layer. Chemical or nutitional factors must, however, be more important in *S.rigescens*, since its sparse trichome layer is very similar to that of *S.hermannii*. The relative contribution of trichomes and phytochemicals to the defence of *Solanum* plants thus seems to vary between different species. Beck (1965) considered plant resistance to be the result of a "partial fit" to "no fit" relationship between the requirements of the insects and the characteristics of the plant. The resistance of *S.mauritianum* to herbivory seems to reflect a "no fit" situation, while a "partial fit" may be reflected in *S.coccineum* and *S.rigescens*. The ecological significance of this "partial fit" is uncertain, as it is not known to what extent herbivore damage is reduced in the field.

## 10.4. Biological control of *S.mauritianum*.

*S.mauritianum* is characterized by a number of vacant food niches in South Africa, since no *Solanum* herbivores were found to exploit these niches. The success of the plant in South Africa can be attributed to the widespread distribution of seeds by frugivorous birds as well as an ability to remain competitive in disturbed areas for longer than most pioneer species. This resilience may be due to several factors. These could include an innate competitive ability, perhaps enhanced by its very low herbivore load. Natural enemies able to minimize the reproductive success of *S.mauritianum* should thus be priority candidates for introduction. Flower-attacking species able to reduce fruit set, as the gelechiid gall-former does on *S.hermannii* (Chapter 6), could prove most useful. An ideal natural enemy would be one able to emulate the effects of the gall-forming pteromalid (*T.acaciaelongifoliae*), which is able to render *A.longifolia* trees virtually sterile (Dennill 1988). Furthermore, the dense stands of existing infestations need to be drastically reduced, by foliage- and stem-associated species, to allow indigenous vegetation and forestry to regenerate.

It would thus appear that a broad spectrum of natural enemies may need to be introduced from South America. The limits of their host ranges need to be carefully determined, considering the wide representation of *Solanum* (particularly those of agronomic importance) in South Africa. The assessment of common *Solanum* herbivores in South Africa revealed a paucity of monophagous species and a predominance of oligophagous types (Chapter 9). Should this trend be reflected in the South American herbivore fauna, selection of suitable natural enemies could prove very difficult indeed. Several South American herbivores tested as biocontrol agents for *S.elaeagnifolium* (Siebert 1975, 1977) and *S.mauritianum* (Neser 1986) were rejected due to insufficient host specificity. The taxonomic distinctiveness of *S.mauritianum* may, however, prove useful as it could prevent some potential agents from switching to indigenous *Solanum* species. Ironically, switching to a narrow range of indigenous plants could prove beneficial, since many of these are problem plants. It is, however, the two cultivated species, potato (*S.tuberosum*) and eggplant (*S.melongena*), which present the greatest potential problems for the introduction of suitable agents.

Both *S.tuberosum* and *S.melongena* are taxonomically distinct from *S.mauritianum*, at the subgeneric level (Table 10.1). However, both species may have lost much of their chemical defence during selection for palatability under domestication. *S.tuberosum* seems generally to be poorly attacked by agents tested for *Solanum* weeds, while the opposite seems to be true for *S.melongena* (Siebert 1975, H.G. Zimmermann pers.comm.). *S.melongena* is notable in that it belongs to a group (section Melongena) which incorporates a number of indigenous species, including *S.hermannii* and *S.panduriforme* (Table 10.1). Observations of *S.melongena* in Grahamstown showed that the three most common folivores of *S.hermannii*, the flea beetle (*Chaetocnema* sp.), tortoise beetle (*C.tigrina*) and ladybird

(*H.hirta*), in addition to other species, inflicted serious damage in vegetable gardens. These observations support the suspicion that *S.melongena*, by virtue of artificial selection, is a "universal accepter" for solanaceous insects (H.G. Zimmermann pers.comm.). If this is true, it is highly unlikely that any monophagous agents will be found for the biological control of *S.mauritianum*. However, the growth forms of *S.mauritianum* and *S.melongena* are very different; for example, *S.melongena* does not display the thick woody stems characteristic of *S.mauritianum*. Certain guilds of insects may thus prove practicable because of these and other differences. Borers which attack only thick woody stems would thus not be likely to transfer to *S.melongena*. Similarly, the fruit of *S.melongena* are vastly different from those of *S.mauritianum* and it seems likely that fruit-attacking agents may also prove relatively safe. However, Siebert (1977) recorded that the pentatomid (*Arvelius albopunctatus* (De Geer)) which was imported to control *S.elaeagnifolium*, attacked the fruit of *S.melongena* in the laboratory although the fruits of the two species are vastly different. The suitability of potential agents can thus only be determined by stringent laboratory tests and not by speculation, although foliage-feeding agents appear to present the greatest risk.

Biological control of *Solanum* species in South Africa may thus have reached a "crossroad" situation requiring a decision on one of two possible appproaches (H.G. Zimmermann pers.comm.). One option would be to abandon all attempts at biocontrol and channel research into alternative methods, particularly herbicides as these have been used to some effect (Neser 1986). Alternatively, the problem could be approached via a thourough examination of the status of cultivated *Solanum* species, particularly *S.melongena*. Laboratory tests on the extent to which indigenous *Solanum* herbivores attack *S.melongena* are required as a standard against which imported agents can be evaluated. Should the preference of indigenous herbivores for *S.melongena* equal or exceed that reflected by imported agents, it could be argued that the possible effects of these agents on eggplant would be minor. A notable point is that pests of potatoes and eggplant are controlled by intensive insecticidal treatments in South Africa (H.G. Zimmermann pers.comm.). Thus, should introduced natural enemy populations be attracted to cultivated species as well as to the target weeds, it is likely that they would be controlled by the insecticide programmes in current use. Should the decision to release imported agents be taken, in spite of their tendency to eat cultivated species in the laboratory, it would be vital to confirm that these agents are susceptable to the particular insecticides used. If not, specific insecticides or additives would, at least, be required as an insurance against transfer to *S.melongena* by introduced agents. Should this general approach be adopted in South Africa, potential agents previously rejected for insufficient specificity should possibly be re-evaluated. The Argentine tortoise beetles, *G.lutescens* and *G.pallidula*, which were rejected as agents for *S.elaeagnifolium* because of their tendency to eat *S.melongena* in the laboratory (Siebert 1975), may thus prove practicable.

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