INSECT HERBIVORES ASSOCIATED WITH *SENECIO PTEROPHORUS* AND *SENECIO INAEQUIDENS* AT BUTTERWORTH, SOUTH AFRICA

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DECLARATION BY CANDIDATE

I declare that this thesis is my own work and that no part thereof has been submitted for any degree to any other university

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ABSTRACT

This study lists and compares insect herbivores of *Senecio inaequidens* and of *Senecio pterophorus* around Butterworth by 18 Tables and 38 Figures. The two plant species are widely distributed around Southern Africa.

Samples were taken during a month of each of the four main seasons of the year, which in Butterworth did not show much difference in temperature.

The two plant species shared generalist insect herbivores most of which were also on other surrounding plant species. The population of most of the herbivores was affected by the seasons while the two plant species were not seasonal, thus the correlation between insect herbivores and the two plant species was not significant.

The heavier, and apparently chemically protected species, *Senecio pterophorus,* accommodated borers and supported a wider variety of but fewer individual insects. *Senecio pterophorus* could be having more defences but had more serious herbivores. There were no serious insect herbivores that could control the abundance of the two plant species around Butterworth.

Anatomical differences between *S. pterophorus* and *S. inaequidens* could be highlighted by the kind and number of insect herbivores found upon them.

Similarities were more difficult to identify through studying their insect herbivores.

The biology of one serious weed, *Lixus* sp., on *Senecio pterophorus* was studied in more detail. The life cycle of the weevil was found to be synchronised with that of the host. This weevil shared the stems with other species of weevils with no indication of competition.

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1 INTRODUCTION

The aim of this research was to compare the insect herbivores of two ecologically and taxonomically related species found in many parts of the world and widely distributed in South Africa. These are *Senecio inaequidens* De Candolle believed by some authors to be synonymous with *Senecio burchelli* L. (common names : English - canary weed; Afrikaans - geelopslag) and *Senico pterophorus* De Candolle that is said to be synonymous with *Senecio polyanthemus* variety *suberratus* L. (common names : Afrikaans - perdigifbos, perdigifbossenecio) (HILLIARD, 1977). The word '*Senicio*' means an old man or groundsel (due to a commonly hoary pappus) (WEBSTER'S DICTIONARY, VOL. III, 1981).

SMALL (1966) believes that *Senecio* was among the basal genera of Compositae and that it originated from Lobelioidae during the late Cretaceous or early Tertiary times in the Bolivian region of South America. The genus *Senecio* belongs to Tribe Senecionae of the Family Asteracea and is said to be the largest genus among angiosperms. (SMALL, 1966; EVERETT, 1980). The number of species in the genus is variously given as 1300 (SMALL, 1966), between 2000 and 3000 (EVERETT, 1980) or 1500 of which 250 occur in South Africa (MABBERLEY, 1969). With so many species it is not surprising that the species in the genus *Senecio* are of very varied morphology and wide distribution.

The genus *Senecio* includes herbs, shrubs, vines, succulents or even trees that exhibit varied lifespans, and grow in many different habitats. Some are ornamentals while others are medicinal herbs used by some South African tribes (JACKSON, 1977).

Senecio species are known to contain poisonous alkaloids such as senecionine and pterophine together with poisonous acids such as senecic acid. These acids and alkaloids together seem to be responsible for poisoning due to *Senecio* plants. (Seneciosis.) The plants are most poisonous during the active growing stage before flowering (GOODWIN AND MERCER, 1983). The strength and quantity of the poison varies with different environmental interactions on a particular species. *S. pterophorus* belongs to the toxic 'ilicifolious' group whereas *S. inaequidens* falls into the non-toxic 'leptophyllus' group (PERSONAL COMMUNICATION WITH D. FOURIE, NATIONAL BOTANIC INSTITUTE, PRETORIA, 1991).

The poisonous effects of *Senecio* plants have been documented by many authors in various parts of the world, including South Africa. Seneciosis has so far been reported in some higher animals such as cattle and horses. For example, 'grass staggers', 'dunsiekte' or 'Molteno disease' in cattle and 'hepatic disease' in horses as a result of eating *Senecio* plants was reported at Mossel Bay and Clan Williams in South Africa. (JACKSON, 1977). The symptoms and post-mortems of seneciosis are described by various authors such as VEHMEIJER (1981), JACKSON (1977) and GULLICK *ET AL.* (1980). JACKSON

(1977) also believes that seneciosis could be responsible for liver cancer in people who use *Senecio* plants as medicine. In the South Western Cape Province of South Africa, the seeds of several species of Senecio were reported to be poisonous when present in flour or baked bread (KING, 1966).

Some insects, however, are able to feed upon or live within *Senecio* plants. It is claimed that insects that feed upon poisonous plants have mechanisms to detoxify or render harmless such poisons (HODKINSON AND HUGHES, 1982). Such insects are expected to specialise on the particular plant species due to the possibility that development of such strategies may have required a long period of coexistence and the alkaloids may even be used by the specialist insect phytophages to recognise their hosts. There is evidence that alkaloids also negatively affect a number of generalist insect species thus lower numbers of generalist herbivore species can be expected. For example, heavy infestations of thrips (Thysanoptera) were found on a species of *Lupinus* lacking alkaloids whereas individuals of the same plant species which contained alkaloids were without thrips. This phenomenon may be due to repellent effects, toxic effects or a combination of the two. The alkaloid tomatine which occurs naturally in a species of *Lycopersicon* (tomatoes) repels the Colorado beetle *Leptinotarsa decemlineata* L. and a leaf hopper, *Empoasca fabae* L. on potatoes *(Solanum tuberosum* L.) but not an *Epilachna* beetle or the grasshopper *Melanoplus bivittatus* L. (HODKINSON AND HUGHES, 1982). Therefore well-protected plant species such as *Senecio* may have fewer herbivores with a higher proportion of specialists than other plants. The toxic *S. pterophorus* may show this effect when compared to the non-toxic *S. inaequidens*.

There are other factors which influence insect species richness and abundance some of which were given as host size, structural diversity and structural complexity by SOUTHWOOD *ET AL.* (1979), MORAN (1980), FOWLER (1985), and STINSON AND BROWN (1982). MORAN (1980) working on *Opuntia* species found host size to account for 35% of variation in insect herbivorous species while structural complexity accounted for 69% of the phytophagous insect species richness although FOWLER (1985) working on birch found that size alone had little impact on species richness of insect herbivores.

The nature of environment might also affect abundance and variety of insect herbivores either directly or by modifying the plant characteristics. SOUTHWOOD (1961) and SOUTHWOOD ET AL (1979) mentioned environmental factors such as density of plants, heterogeneity of plant species in the area and the ability of a plant species to grow in a variety of habitats. LEWIS (quoted in STRONG, *ET AL.*, 1984) stated that barriers to air flow such as hills and ridges, buildings, trees, hedges and even canopies of other plant species create sheltered zones in which insects accumulate while insects are dislodged when exposed to strong winds.

HODKINSON and HUGHES (1982) showed that when an insect species fed on two plant species only this implied taxonomic relatedness between the two plant species and if an insect fed upon two plant species and also other plant species this indicated both taxonomic and ecological relatedness. *S.pterophorus* and *S. inaequidens* share habitats in some regions where they are both recorded such as in North and South America and in South Africa (HILLIARD, 1977). However, *S. inaequidens* appears to be more widely distributed around the world than *S. pterophorus* as it is recorded without *S. pterophorus* in northern Italy, West Germany (HUELBUSCH AND KUHBIER, 1979), France, Belgium, Britain and Namibia (HILLIARD, 1977). *S. pterophorus* (without *S. inaequidens*) is reported only in southern Australia (HILLIARD, 1977).

Since it is mainly insects which successfully feed upon these two plant species, insects may play an important role in determining their abundance. Little entomological work has so far been directed towards *S. pterophorus* and *S. inaequidens*.

Results from this study would be used to establish whether insect herbivores influence the abundance and perhaps distribution of these two important plant species.

2. MATERIALS AND METHODS

2.1 STUDY AREA

The study was carried out in the Butterworth district of Eastern Cape which lies between 27° and 30° East, and between 30° and 33° South. The following information concerning Butterworth district and surrounding areas is as given by Swanevelder *et al.* (1975);

Altitude : between 50m and 760m.
Temperature : mean maximum = 23°C, and
mean minimum = 16,7°C.

Highest temperature occurs in January while the lowest temperatures occur in June.

Precipitation : annual rainfall ranges from 140mm to 750mm,
69% to 73% falling during summer.

There is frost, during winter and fog any time of the year at Butterworth.

The study area is basically agricultural with a number of small farms and many settlements with mainly cattle and sheep but also a few goats and horses. The population density of people is relatively high and some industrialisation is taking place.

2.2 THE STUDY

A preliminary survey of the insect herbivores of the two species at a range of sites was followed by the main, seasonal, sampling at two sites selected from these. In addition, a biological study was conducted upon the stem borers of *S. pterophorus*.

2.2.1 THE PRELIMINARY SURVEY

Preliminary surveys were conducted from December 1984 to June 1986 with the aim of identifying suitable sites for sampling, determining the nature of the insect herbivores and the best methods for sampling and analysing them. Certain attributes of the two plant species were also determined. This survey involved a general collection of insect phytophages at six sites, A, B, C, D, E and F.

Site A was in and around a gently sloping, mainly grassy area with no livestock, a few shrubs and no trees.

Site B was 15km west of Butterworth, beside the road to the Kei Bridge. Site B was formerly a farming area although some livestock were still present. The two plant species disappeared from this site in late 1985 when later successional communities took over the area.

Site C was in and around the Butterworth Forest Reserve. Both plant species disappeared there in December 1985 but reappeared in April 1986.

Site D was a grazing area with scattered shrubs, between 7 and 10km from Butterworth towards Idutywa.

Site E was along the margin of the Nqamakwe Forest Reserve. This was a very fertile area with dense vegetation and nearby crops of maize.

Site F occupied a clayey swampy area showing signs of previous cultivation but at present a grazing area. A river passed through this site.

From January 1985 until October 1985 two plants of each species were collected per month from each site, giving a total of 12 plants of each species per month and an overall total of 120 plants of each species from all the six sites mentioned above. Each plant was initially examined for active insects which were collected as follows; a plastic garbage bag was carefully lowered over the plant and the mouth of the bag tied around the base of the stem. The plant was then cut at the soil level and the roots dug up and stored in another bag.

To quantify some of the physical attributes of the two plant species, the 120 plants of each species mentioned above were used. The circumference of the stem was measured at ground level and the pith width at 1cm, above ground level. The height of the plant was determined by stretching a measuring tape from the ground level along the stem up the highest point of the plant. The plant density was taken by throwing a metre-square over an area containing both plant species and then counting the plants of each species enclosed in the metre-square, twice in each of the six sites.

A second preliminary survey was conducted to determine the number of plants per sampling occasion which would adequately sample the insect herbivores that feed upon each plant species. For *S. pterophorus* 25 plants were picked over three days during December 1985 and another 25 plants on different dates during June 1986, giving an overall total of 50 plants. The same procedure was carried out for the smaller *S. inaequidens* except that 30 plants were collected on each of the occasions. The plants in each sample of 25 or 30 were searched one by one, and cumulative totals of herbivorous insect species added. Figs. 1(a) and 1(b) represent the cumulative number of herbivorous insect species collected during this preliminary survey.

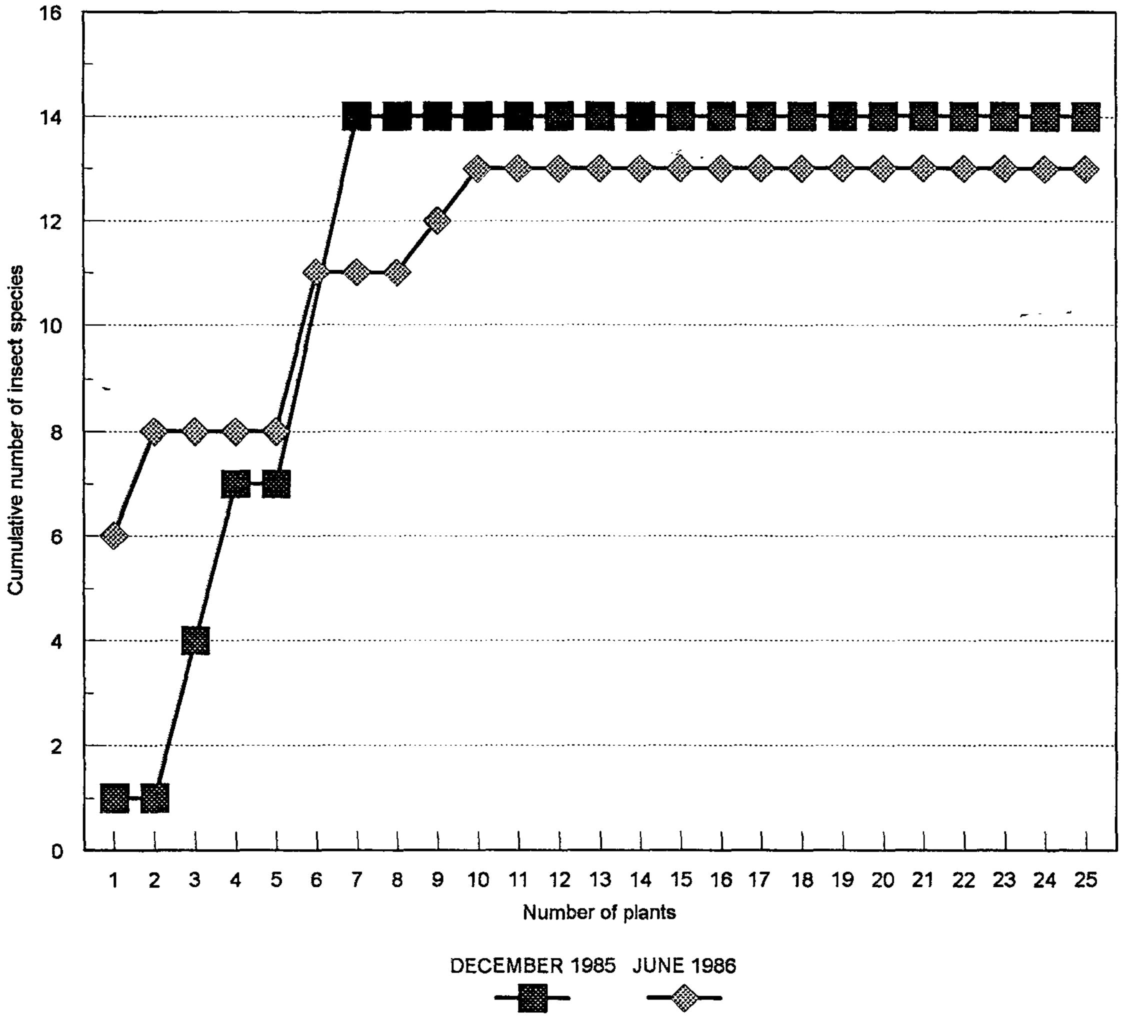


Fig. 1(a) Number of herbivorous insect species on *S. pterophorus* (preliminary survey)

Note : 1 The shape of the slope leading to the maximum, but note the maximum value, would change if the plants involved had been picked in a different sequence.

2 Where the number of species remained the same there was no additional, or new, species found on that plant but there could have been insect species upon that plant which had already been found upon the plants earlier, or there could have been no insect at all.

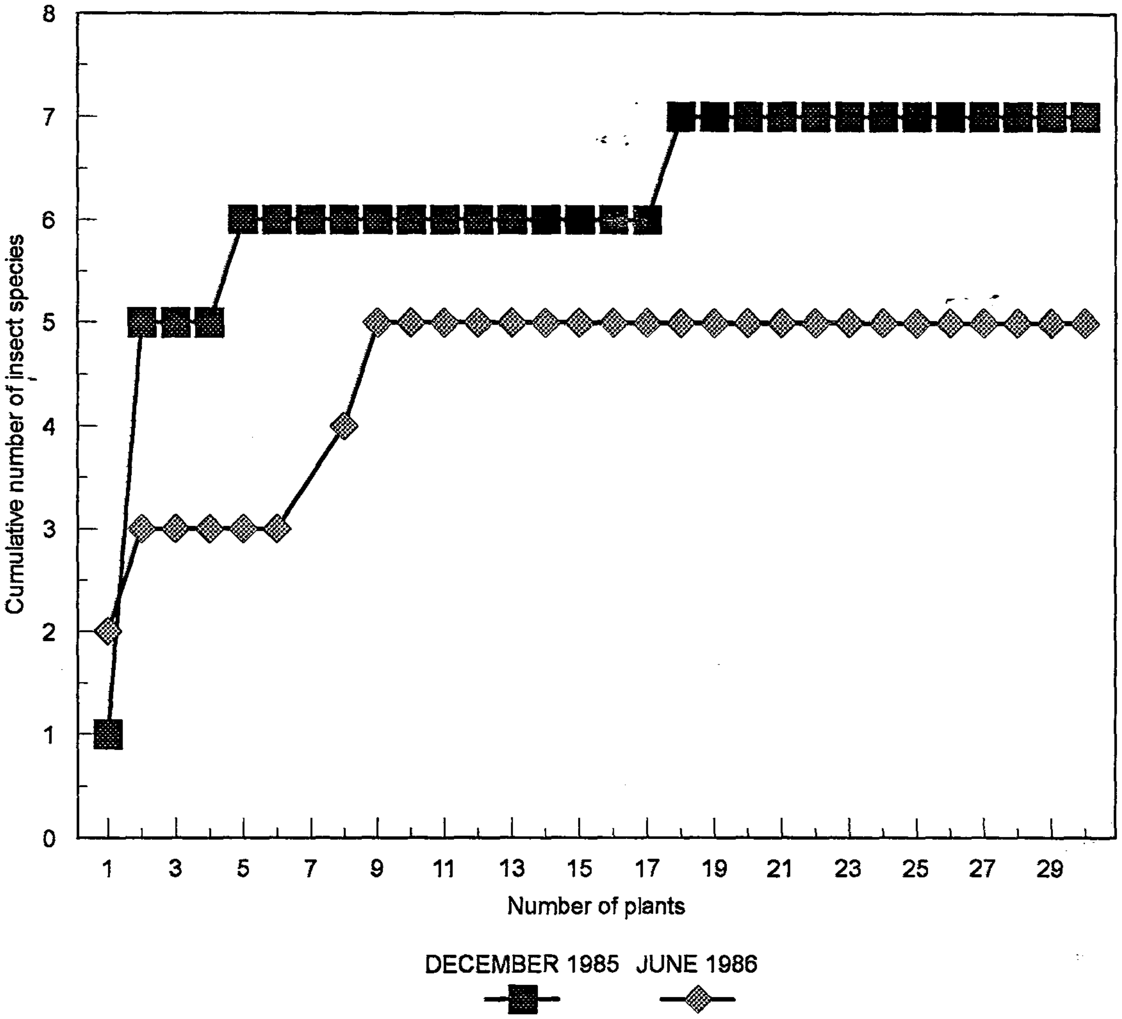


Fig. 1(b) Number of herbivorous insect species on *S. inaequidens* (preliminary survey)

Note : 1 The shape of the slope leading to the maximum, but note the maximum value, would change if the plants involved had been picked in a different sequence.

2 Where the number of species remained the same there was no additional, or new, species found on that plant but there could have been insect species upon that plant which had already been found upon the plants earlier, or there could have been no insect at all.

2.2.2 THE MAIN SAMPLING PROGRAMME

Based on the results of the preliminary samples the main sampling was conducted as follows in Sites A and F only which were chosen for proximity to the laboratory. Sampling was carried out in all four seasons, in July, October, January and April. Plants were collected as described above for the preliminary sampling. An initial plant was collected and then the direction of the next plant was determined by picking labels marked either left, right or straight ahead from a paper bag. Two hundred steps were then taken in that direction and the nearest plant sampled. The process was repeated until the desired number of plants had been collected. The number of plants per sample at each site for *S. pterophorus* was 16 and for *S. inaequidens* 32, much more than the numbers realised during the preliminary survey.

Special attention was paid to the stem borers because of their potential for causing more serious damage to *S. pterophorus* than, for example, folivores. The methods of sampling stem borers are given in Chapter 6.

2.3 PROCESSING OF SAMPLES

Immature stages were reared for further identification. Most of these were larvae and pupae extracted from dissected flowers and stems. This rearing also included free immature insects from the plant surface.

2.3.1 REARING CAGES

Plastic soft drink bottles of about 2-litre capacity and 5cm, diameter were used as rearing containers. (Appendix I).

The bottom was cut off and the bottle was then fitted with a tightly fitting sponge which was about 3cm thick but with a small hole in its centre for insertion of the plant stem. The stem of a freshly collected plant, carefully cleared of insects, was cut above the root and immediately fixed in the sponge which was at the time soaked with fresh water. Then the plant and sponge were fitted into the bottle. The sponge and the bottle stood in a saucer containing water. The lid of the bottle was replaced by a gauze cloth to allow ventilation. A sample of each larva or pupae was preserved in alcohol for reference. Better results were achieved when the plant stem was cut and fixed in the sponge under water. Precautions taken to reduce fungal infection included keeping the humidity low and keeping the bottled specimen well aerated. Insects were transferred to fresh plants when necessary. For recovery of the emerged adult insects, the gauze was replaced by a vial and the bottle was placed in a black plastic bag with the mouth protruding and placed under a powerful reading lamp. Some were also raised in cages on potted plants. (Chapter 6.).

2.3.2 EMERGENCE CONTAINERS

Wine-bottle sleeves were used where pupation or emergence of the collected insects was expected in a short time. The emergence container is shown in Appendix II. A hole was made in the base of the sleeve and a vial lid whose centre had been removed was then glued over it. A vial was attached to the lid. Shoots and flowers were then inserted through the open end which was then closed by wedging in the base of a second sleeve. Insects entering the vial could then easily be collected. Apart from raising larvae that were close to pupation this method was also used for recovery of free insects on the flowers and shoots. A weakness of this method was that one could not monitor the activities of the insects because the sleeves were opaque and also by the time samples were removed the material was too dry to recognise and identify types of damages correctly.

2.3.3 EGGS, LARVAE AND PUPAE OF ENDOPHAGOUS INSECTS.

Mature larvae and pupae were reared between layers of moist tissue paper inserted into a well-ventilated, gauze covered, vial at room temperature. Mature larvae and pupae of Diptera responded to this method favourably.

A satisfactory method for stem borers (except Cerambycidae) was to introduce the larva or pupa into 10cm long pieces of *S. pterophorus* stem, the pith of which had been partly removed. The borer was inserted, head first and removed when the stem-piece was becoming dry.

Potted plants covered with a muslin gauze were used to rear nymphs and mobile juveniles such as thrips. Alternatively, small muslin bags were used to cover shoots or flowers inside which a single selected insect species was introduced.

The two later methods were employed particularly for studying life-cycles and feeding habits of some hemipterous species.

Borer species could grow in a mixture of sawdust and maize flour at a volume ration of 1:1. Sawdust was heated to kill micro-organisms and on cooling was mixed with maize flour. The mixture was poured in a tray of about 3cm deep, covered with muslin gauze and a little water was added to keep the mixture moist. The three species of borer larvae grew in size in this mixture but could not develop further to pupate until placed in the pieces of stems of *S. pterophorus* as described above (except the species of Cerambycidae). It was established that an increase in the proportion of maize flour and adding more water which would subsequently be evaporated by placing the mixture in the sun whilst the mixture was already in the tray resulted into a harder solid through which borer larvae could make burrows similar to the ones they made in the stems of *S. pterophorus*. The best volume ration of sawdust, maize and water was not investigated further since the stems pieces of *S.*

pterophorus worked well in developing borer larvae. This mixture was sometimes used to grow very small borer larvae up to a size that could easily be inserted in stem pieces described above.

3. THE PLANT SPECIES

3.1 INTRODUCTION

This chapter deals with aspects of the biology of *S. pterophorus* and *S. inaequidens*. It comprises of data from HILLIARD (1977) as well as observations made during the preliminary survey in the six sites.

3.2 IMPORTANT ASPECTS OF THE MORPHOLOGY AND ANATOMY OF *S. pterophorus* AND *S. inaequidens*

S. pterophorus is a herb that grows to a maximum height of approximately 2m with a woody stem having a pith of variable diameter. This height gives it prominence among pioneer communities in which both plant species are often found. Leaves are covered with trichomes and reach a size of about 15cm x 4cm. The yellow flower heads are radiate with many flowers growing on short bracteate penduncles arranged in spreading corymbose panicles.

S. inaequidens is a shorter herb and may grow to a maximum height of approximately 1m. It may be bushy or not, branching vigorously from the base of the stem. The foliage may touch the ground. Flowers are yellow, radiate and with bracteate peduncles as in *S. pterophorus* but in the case of *S. inaequidens* there are fewer flowers on each peduncle. The peduncles are longer and the corymbose panicles are open. The leaves of *S. inaequidens* are smooth and exhibit a variety of shapes, the maximum size of which was found to be 10cm x 3cm. Its stem is thinner but the pith is proportionately of greater diameter compared to the stem diameter than in the case of *S. pterophorus*.

Measurements taken during the preliminary survey appear in Table 1.

TABLE 1 **Results of a survey of some attributes of flowering plants of *S. pterophorus* and *S. inaequidens* obtained between December 1984 and June 1986 in the 6 sites.**
(Sample size = 20 plants per site; S.E. in brackets following means.)

	SITE	MEAN STEM CIRCUMFERENCE / CM		MEAN PITH WIDTH / CM		MEAN HEIGHT / M		DENSITY / M^2	
SPECIES		*S. PTERO*	*S. INAEQ.*	*S. PTERO*	*S. INAEQ.*	*S. PTERO*	*S. INAEQ.*	*S. PTERO*	*S. INAEQ.*
	A	3,7 (0,41)	1,0 (0,06)	0,20 (0,51)	0,21 (0,05)	0,60 (0,20)	0,29 (0.97)	0,01 (1,31)	0,01 (0,80)
	B	4,1 (0,33)	1,0 (0,13)	0,31 (0,04)	0,18 (0,21)	0,98 (0,02)	0,35 (0,71)	5,00 (0,84)	0,09 (0,72)
	C	4,5 (0,22)	1,8 (0,30)	0,23 (0,20)	0,14 (0,04)	1,13 (0,10)	0,46 (0,61)	8,00 (0,93)	0,03 (0,60)
	D	4,7 (0,10)	1,4 (0,07)	0,24 (0,70)	0,23 (0,20)	0,10 (0,03)	0,42 (0,02)	3,00 (1,60)	0,01 (0,50)
	E	5,0 (0,08)	1,6 (0,11)	0,24 (0,03)	0,10 (0,51)	1,32 (0,70)	0,55 (0,03)	1,00 (1,20)	0,01 (0,32)
	F	4,8 (0,35)	2,2 (0,40)	0,21 (0,04)	0,16 (0,62)	1,21 (0,50)	0,48 (0,04)	7,00 (1,70)	2,01 (0,53)
OVERALL MEAN		4,5 (0,17)	1,5 (0,17)	0,24 (0,01)	0,17 (0,02)	0,86 (0,18)	0,43 (0,02)	4,00 (1,20)	0,36 (1,10)

3.3. SPECIFIC NATURE OF THE HABITAT AROUND BUTTERWORTH

Both plant species grow in recently disturbed areas although *S. inaequidens* is much more dependent on recently cleared areas than *S. pterophorus. S. inaequidens* could be found amongst crops and flower gardens probably due to its smaller size. It established itself more quickly in new disturbed areas than *S. pterophorus.* It was also common in shade (either from man-made structures such as bridges or under bigger plants, including *S. pterophorus*) and along edges of damper areas such as road sides, drainage systems and small streams. *S. inaequidens* was never seen on hill tops but was also not found in water-logged places such as swamps.

S. pterophorus was found in all pioneer situations characteristic of *S. inaequidens* but also in drier areas and this implies everywhere in and around Butterworth.

Other common plants which were often growing with the two *Senecio* species in the study area were *Bidens pilosa* L., *Bidens bipannata* L., *Cirsium vulgare* Savi, *Taraxacum officinale* Web., *Galinsoga parviflora* Car., *Amaranthus* sp., *Angremona* sp., *Eurypus floribundus* L., *Plantago major* L., *Ursinia narra* L., *Solanum nigrum* L., *Dreygnsia nordmannis* L., *Digitaria* sp., *Urocholoa helopus* Staff., *Cynodon dactylon* Pers., *Eleusine indica* Gaerth., *Themeda triandra* L. and *Cyperus esculentus* L.

The main cash crops in the area included maize, sorghum and sun flowers (sharing the same tribe as *Senecio*.)

3.4 DISTRIBUTION IN SOUTHERN AFRICA

The current distribution of *S. pterophorus* and *S. inaequidens* in Southern Africa is illustrated in Figs. 3 and 4 respectively using data supplied by DE WET (1991) of the National Botanical Institute, Pretoria. That data did not include Butterworth, East London, Komga, Idutywa and Umtata although the two plant species are found there. This observation was brought to the notice of the National Botanical Institute, Pretoria.

Other specific areas have been indicated by various authors which may not appear in the distribution map. ADAMS AND SALTER (1950) quoted a report of *S. pterophorus* before 1918 at Newlands - Rondebosch (where it was hybridising with *S. rigidus* L.) and they, in 1950, reported it between Camps Bay and Kirstenbosch. GUILLARMOD (1971) reported *S. inaequidens* with its sub- species in Lesotho (at Cana, Berea, Thaba Bosiu and Maseru). JACKSON (1977) reported *S. pterophorus* on Table Mountain - Cape Town. The most comprehensive distribution records of both plant species were given by HILLIARD (1977) who believed that they were spreading and were likely to become serious weeds. Apart from areas reported by earlier authors, HILLIARD (1977) included the eastern part of Transkei, the southern part of Natal (including Weza Forest Reserve) and between Umsikaba and Umzimkulu.

S. inaequidens is more widely distributed than *S. pterophorus* but lacking around the Cape Peninsula and surrounding areas whereas *S. pterophorus* is generally along the coast from Cape Town towards Swaziland and the Eastern Transvaal. (Figs. 2 and 3).

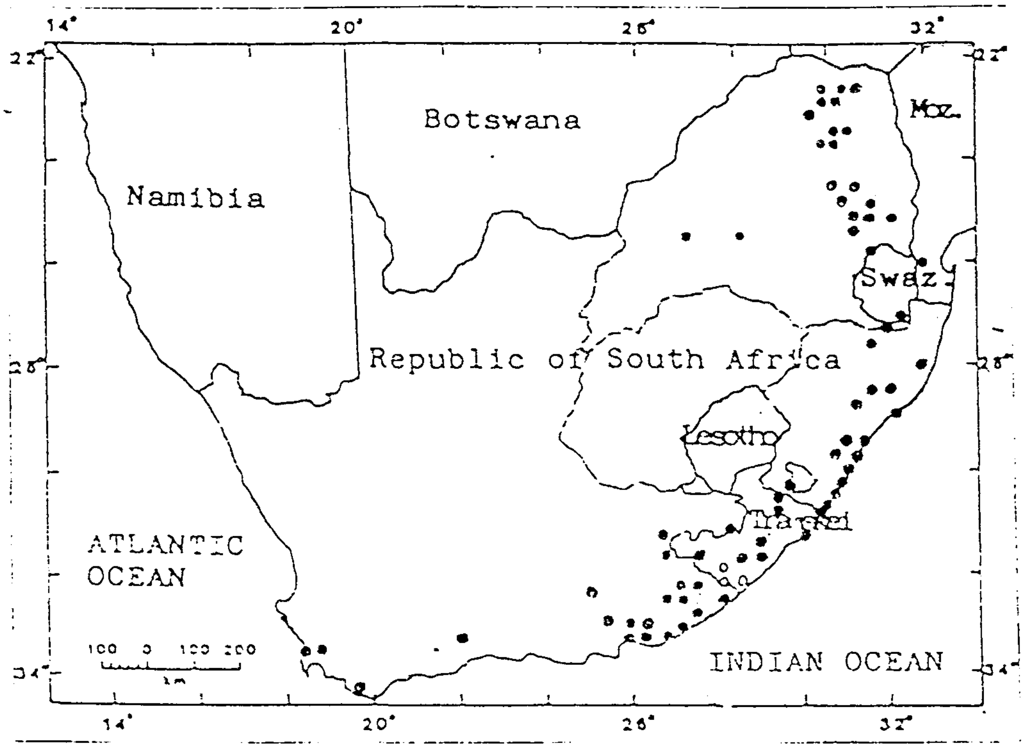


Fig. 2. Distribution of *S. pterophorus* in South Africa. Records which were obtained from De Wet of the National Botanic Institute in Pretoria are represented by closed circles. The open circles represent areas from which specimens were collected during this research programme. Specimens were indentified by the National Botanical Institute.

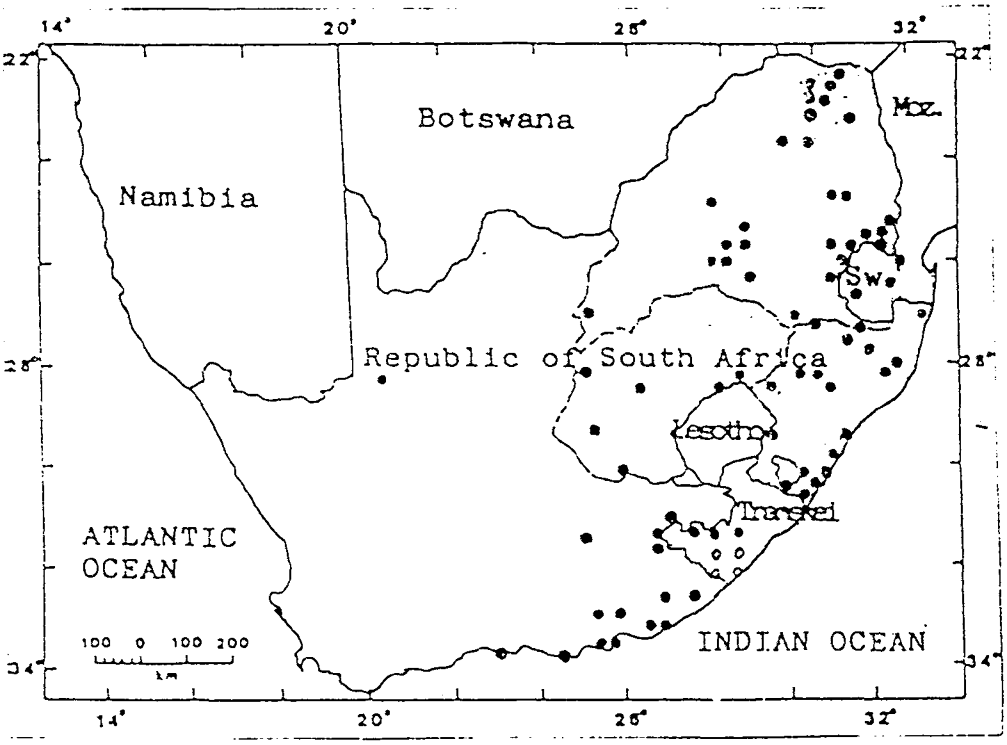


Fig. 3. Distribution of *S. inaequidens* in South Africa. Records which were obtained from De Wet of the National Botanical Institute in Pretoria are represented by closed circles. The open circles represent areas from which specimens were collected during this research programme. Specimens were identified by the National Botanical Institute.

3.5 SEASONAL DISTRIBUTION

There were no strict seasonal patterns in relation to the phenology of *S. inaequidens*. For example, germination was more determined by the availability of disturbed bare ground accompanied by good rains, than by season. This pattern was less evident with *S. pterophorus*, where seasonality was also important. *S. inaequidens* could flower within 5 months of germination during any season. Populations in areas where rain or other forms of water were plentiful showed all stages of development such that mature flowering plants were available throughout the year. This was true for both study sites.

Although mature plants could flower during any time of the year, the main flowering months were March, April, September, October and November in case of *S. pterophorus*, which seemed to be more sensitive to seasons than *S. inaequidens*.

While *S. inaequidens* was purely annual, *S. pterophorus* exhibited both annual and biennial cycles. Factors which led to the biennial alternative were not clear but it appeared that this happened when there was no competition from other plant species. For example, all the 26 plants in a residential backyard and 8 in pots, planted for rearing juvenile insects, under no competition, followed a biannual cycle. Among those planted the longest lifespan was 21 months for *S. pterophorus* and 8 months for *S. inaequidens*.

Also in the field where other plants had died of frost or fire, *S. pterophorus* plants took on a second cycle of growth.

3.6 IMPORTANCE OF THE TWO *SENECIO* SPECIES

Wells *et al.* (1986) listed both species as pastures, flower gardens, crops and health weeds. They can cause stock and human life loses due to their poisonous nature. (Chapter 1).

As pioneer plants they may help to cover bare ground quickly and so contribute towards a reduction in soil erosion and towards and early increase in organic content of the area upon which later organisms can rely for their establishment.

They could be alternative hosts for pests of sunflowers (which share the same tribe as *Senecio*) or maize and sorghum which are the main cash crops around Butterworth.

4. INSECTS ASSOCIATED WITH *S. pterophorus* AND *S. inaequidens.*

4.1 INTRODUCTION

The number of species and kind of guilds of insects that are found upon a plant may be important in highlighting the taxonomic differences, or similarities, between two plant species (Hodkinson and Hughes, 1982). Goeden and Ricker (1967, 1976) mentioned the value of using faunistic surveys to determine whether a plant species was indigenous or exotic, while Southwood *et al* (1979) said that such surveys can be used to evaluate and compare the ecology or physical proximity of plant species.

The feeding guilds may also be used to analyse the anatomy of a host.

Both plant species were shown by both the preliminary survey and seasonal samples to have quite extensive insect faunas. The diversity of the phytophages of the two species was evaluated and compared to highlight the differences and similarities,in the various ways mentioned above,between the two plant species.

4.2 RESULTS

Results indicated a high degree of similarity of insect herbivores between the two plant species and also between sites.

4.2.1 RESULTS OF THE PRELIMINARY SURVEY

Insect yields varied at all sites (A, B, C, D, E and F) during the different months. However, sites A and F yielded greater numbers of individuals although there was no qualitative differences of insect herbivores between sites.

Preliminary survey results were used to identify common generalists found on so many other plant species and those which were not regular, such as grasshoppers and caterpillars. Such insect herbivores were not listed among the samples since no clear and serious association was observed.

4.2.2 RESULTS OF THE FOUR SEASONAL SAMPLES

Results of the four seasonal samples are given in Table 2 below. *S. pterophorus* recruited 4 more species of insect herbivores but *S. inaequidens* had a higher number of insects per 100g dry mass of every part of the plant. The combined results of the seasonal surveys at Sites A and F indicated a variety of feeding guilds which exploited all of the parts of each plant species.

Table 2 shows that there were 18 phytophagous insect species upon *S. inaequidens,* all of which were generalists and that some of these were found among the 22 insect phytophages which were collected from *S. pterophorus* although this plant species recruited three stem borer species all of which seemed to be more monophagous in all the seasonal samples and gave *S. pterophorus* an extra feeding guild that was absent in *S. inaequidens*.

This number of herbivorous species was low compared to that of other plant taxa. For example, OLCKERS (1988) recorded between 15 and 32 species of insect herbivores on various species of *Solanum* in South Africa, while GOEDEN AND RICKER (1967, 1976) collected 91 species on *Salsola kali* var. *tennifola* and 113 species from *Ambrosia psilostachya* respectively. However, OLCKERS (1988) and GOEDEN AND RICKER (1967, 1976) used more samples and for a longer period both of which factors may increase the number of recruited herbivores. Although more samples from other sites elsewhere are necessary for a complete assemblage of species of insect herbivores associated with the two *Senecio* species, the duration of this investigation was satisfactory for and was seasonally representative of insect herbivores associated with the two *Senecio* species at Butterworth. Monophagous insect herbivores would have appeared and their low numbers or absence would be an indication of either the unpalatability of *Senecio* in relation to other plant species in the area or an indication of the possibility that the two *Senecio* species are new inhabitants at Butterworth. That the two *Senecio* species could have just spread into Butterworth is supported by the fact that the National Botanical Institute at Pretoria and various authors listed in Chapter 3 (see page 21) did not include Butterworth and surrounding areas among the places where the two *Senecio* species could be found, and HILLIARD (1977) believed that the two plant species were spreading.

TABLE 2. **Number of insect herbivores per 100g dry mass of each of the parts of host plants. The numbers in parentheses represent the number of seasons out of a total of four seasons in which each insect species was represented.**

	S. pterophorus	*S. inaequidens*
FLOWERS	No of insects / 100g dry mass of flowers	
THYSANOPTERA		
Thripidae (thrips)	177.3(4)	462,0(4)
HETEROPTERA		
Lygaeidae		
Nysius natalensis Evans (ACRH 605)	5,6(3)	26,6(2)
Spilostethus sp. (ACRH 435)	57,3(4)	43,1(4)
HOMOPTERA		
Aphididae (probably *Myzus* sp.) (ACRH 442)	Very Many (4)	Very Many (4)
COLEOPTERA		
Chrysomelidae		
Criocerinae		
Oulema bilineata Germar (ACRH 597)	-	7,3 (2)
Galerucinae		
Monolepta sp. (ACRH 432)	5,6 (2)	11,3 (2)
Cryptocephaline		
Cryptocephalus decemnotatus Suf. (ACRH 596)	-	31,9 (2)
(ARCH 434) - small and black	192,4 (4)	185,9 (4)
Phalacridae (ACRH 594)	24,7 (3)	18,6 (4)
Melyridae		
Astylus atromaculatus Blanchard (ACRH 595)	-	13,3 (2)
Cetoniinae		
Leucocelis sp. (ACRH 587)	12,7 (2)	12,6 (2)
Meloidae		
Decapotoma sp. (ACRH 593)	-	2,7 (2)
Cerostis capensis L. (ACRH 441)	2,4 (2)	-

	S. pterophorus	*S. inaequidens*
FLOWERS	No of insects / 100g dry mass of flowers	
Lycidae		
Lycius sp. (ACRH 586)	10,3 (2)	-
Scarabaeidae		
Hopliinae		
Monochelus sp. (ACRH 440)	3,2 (2)	-
Heterochelus sp. (ACRH 437)	2,4 (2)	-
Trichiinae		
Strisipher flavipenis Gory and Percheron (ACRH 438)	4,0 (2)	-
DIPTERA		
Drosophilidae (ACRH 598)	15,1 (2)	17,9 (3)
Tephritidae		
Trupanae incisa Munro (ACRH 599)	5,6 (2)	9,3 (4)
FOLIAGE	**No of insects / 100g dry mass of foliage**	
HETEROPTERA		
Lygaeidae		
Nysius natalensis Evans (ACRH 605)	0,4 (4)	8,2 (3)
Spilostethus sp. (ACRH 435)	0,2 (4)	11,9 (4)
Pentatomidae		
Agonoscelis versicolor F. (ACRH 588)	0,6 (4)	-
HOMOPTERA		
Aphididae (aphids) (ACRH 442)	very many (4)	very many (4)
COLEOPTERA		
Chrysomelidae		
Cryptocephaline		
Cryptocephalus decemnotatus Suffrian (ACRH 596)	-	5,5 (2)
Eumolopinae		
Pseudoclapsis sp. (ACRH 600)	-	3,6 (4)
Criocerinae		
Oulema bilineata Germar (ACRH 597)	-	11,7 (3)
Crysomlidae		
Galerucinae		

	S. pterophorus	*S. inaequidens*
Monolepta sp. (ACRH 432)	1,1 (2)	13,8 (1)
Melyridae		
Astylus atromaculatus Blanchard (ACRH 595)	-	1,1 (4)
Cerambycidae		
Promeces sp. (ACRH 585)	0,1 (2)	-
Curculionidae		
Lixus sp. (ACRH 581)	0,1 (2)	-
Mordellidae		
Mordella sp. (ACRH 580)	0,1 (1)	-
Elateridae		
(ACRH 444)	0,1 (2)	-
STEMS	**No of insects / 100g dry mass of stems**	
HETEROPTERA		
Coreidae		
Anoplocnermis curvipes F. (ACRH 591)	-	2,6 (3)
Cletus sp. (ACRH 589)	-	4,8 (2)
HOMOPTERA		
Aphididae		
aphids (ACRH 442)	very many (2)	very many (4)
Tettigometridae		
Hilda patruelis Stal (ACRH 584)	0,1 (2)	32,5 (4)
COLEOPTERA		
Curculionidae		
Lixus sp. (ACRH 581)	0,1 (4)	-
Mordellidae		
Mordella sp. (ACRH 580)	0,1 (4)	-
Cerambycidae		
(larvae only)	0,3 (4)	-
ROOTS	**No of insects / 100g dry mass of roots**	
HOMOPTERA		
Tettigometridae		
Hilda patruelis Stal (ACRH 584)	18,3 (4)	214,1 (4)

Table 2 above also shows that for both plant species herbivore species richness diminished from flowers to foliage, to stems and to roots. *S. pterophorus* accommodated four more insect species in total than *S. inaequidens* with an extra species on all parts except the roots. (Table 3). The single species which was found upon roots was shared by both plant species. The second highest rate of sharing was realised upon flowers followed by foliage and stems.

Shared herbivores were equally regular (i.e. were represented in the same number of samples) except Phalacridae (ACRH 594), Drosophilidae (ACRH 598), Aphids (ACRH 442) and *Hilda patruelis* Stal which appeared in more samples on *S. inaequidens*.

TABLE 3. A comparison of the number of herbivorous insect species on the different parts of the two plant species (percentage of species shared in parentheses).

Part of Plant	***S. pterophorus***	***S. inaequidens***	**No. of species shared.**
Flowers	15 (66,7%)	14 (71,4%)	10
Foliage	9 (44,4%)	8 (50,0%)	4
Stems	5 (40,0%)	4 (50,0%)	2
Roots	1 (100,00%)	1 (100,00%)	1
The Whole Plant	22 (50,0%)	18 (61,1%)	11

Although S. *inaequidens* appears to have a higher percentage of its insect herbivores shared on all parts, except roots, they wereagain significantly different from the percentages of shared insect herbivores of *S.pterophorus* (for MANN - WHITNEY "U" = 2 and $n_1 = n_2 = 3$, one - tailed $p = 10\%$, thus $p > 5\%$)

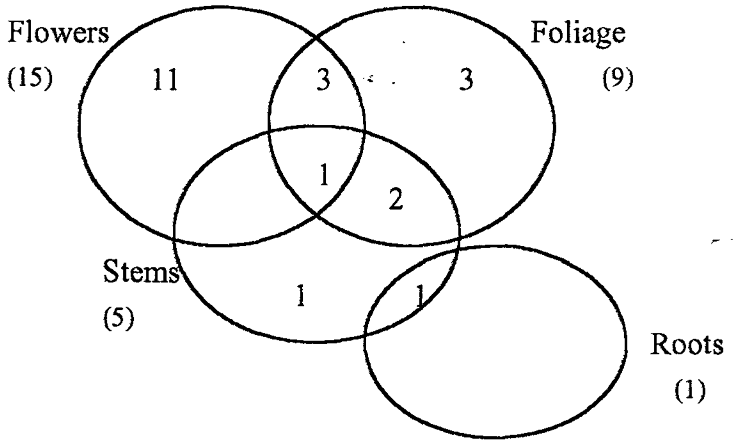
The faunal overlap on the different parts of the plant was higher upon S. *inaequidens* than on S. *pterophorus* particularly between the flowers and the foliage (Table 4 and Fig. 5). No insect species was found on all four different parts of the two plant species thus indicating that the different parts were probably of very different texture each of which required a different kind of feeding.

TABLE 4 Insect herbivore overlap over the different parts of the two plant species.

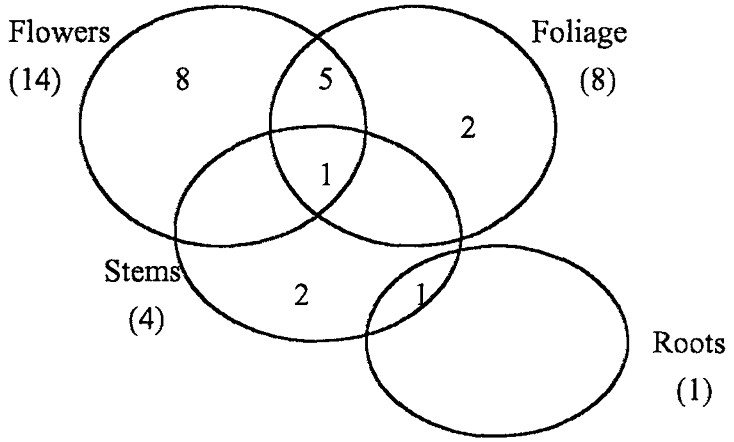
	Number of herbivorous insect species	
Part of the Plant	***S. pterophorus***	***S. inaequidens***
Flowers, foliage and stems	1	1
Flowers and foliage	4	6
Foliage and stems	3	1
Stems and roots	1	1

Note : Parts which never shared insect herbivores were left out of Table 4.

The overlaps also highlighted the neighbourhood effects - that neighbouring parts may share herbivores.



Faunal overlap on *S. pterophorus*



Faunal overlap on *S. inaequidens*

Fig. 4 Venn Diagrams to illustrate the overlap of insect herbivores

Note 1 Numbers refer to number of herbivorous insect species.

2 The Venn diagrams are based upon Tables 3 and 4.

Figs. 5 and 6 show that the two plant species recruited insect herbivores from the same Orders and both almost in the same proportions. On both plant species the number of herbivorous insect species diminish from Coleoptera to Heteroptera, to Homoptera and Diptera down to Thysanoptera. Both plant species lacked members of Collembola, Hymenoptera and Phasmida among the less generalist phytophagous Order of insects.

Figs. 5 and 6 also show the number and percentage of insect herbivores in each feeding guild that were collected from *S. inaequidens* and *S. pterophorus* respectively. The majority were chewers followed by sap suckers on both plant species. *S. inaequidens* had proportionately more sap suckers while *S. pterophorus* had a bigger proportion of chewers. Borers were not found in *S. inaequidens* thus this plant species had less feeding guilds.

The proportion of ectophagous (sap suckers, chewers and pollen eaters) insects was 88,9% for *S. inaequidens* but 86% for *S. pterophorus* because the later probably due to its larger size recruited additional endophages, the borers apart from saprophages, although the difference is not that much. However, the proportion of ectophages is comparable to, for example, 73% that was found on larger plant species *Solanum* by OLCKERS (1988) . More samples would be required elsewhere to make a justified comparison of guilds which would be determined by the environmental factors in such areas, especially for generalists.

That none of the guilds caused considerable damage may imply that the two plant species were under utilised and could still be having vacant niches in support of the "pool exhaustion" hypothesis by STRONG *ET AL* (1984). Analysis of ectophages revealed a predominance of sap suckers upon *S. inaquediens* (33,3%) compared to that on *S. pterophorus* (25%) while more chewer species were found on the later plant species (55%) compared to the (50%) of the former. That analysis can be used to compare the texture of tissue of the two plant species since sap suckers would most likely go for softer tissue such as those of *S. inaequidens* while chewers could manage soft and hard tissues but would probably find less competition on the harder tissues of *S. pterophorus* even though its foliage was protected by trichomes while other tissues could have had chemical protections by the poisonous alkaloids (mentioned in Chapter 1).

Figs. 7 and 8 show the number of insect herbivores/100g. dry mass of plant in each feeding guild for *S. inaequidens* and *S. pterophorus* respectively. For every feeding guild, except borers, more insects/100g dry mass of plant material was found upon *S. inaequidens* implying that this plant species was less protected from insect herbivory.

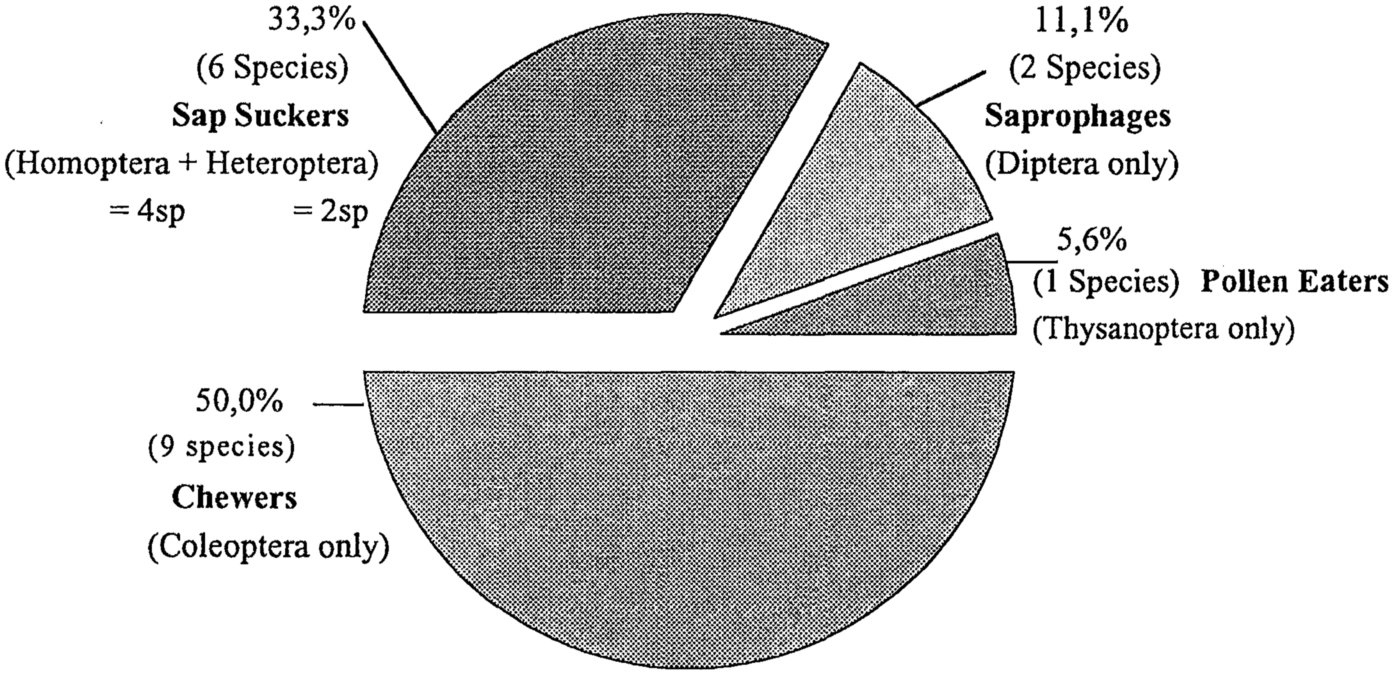


Fig. 5. The percentage of herbivorous insect species of each feeding guild that were found upon *S. inaequidens.*
The number of insect species in each feeding guild is placed in parentheses.
18 herbivorous insect species were found upon *S. inaequidens* in total.

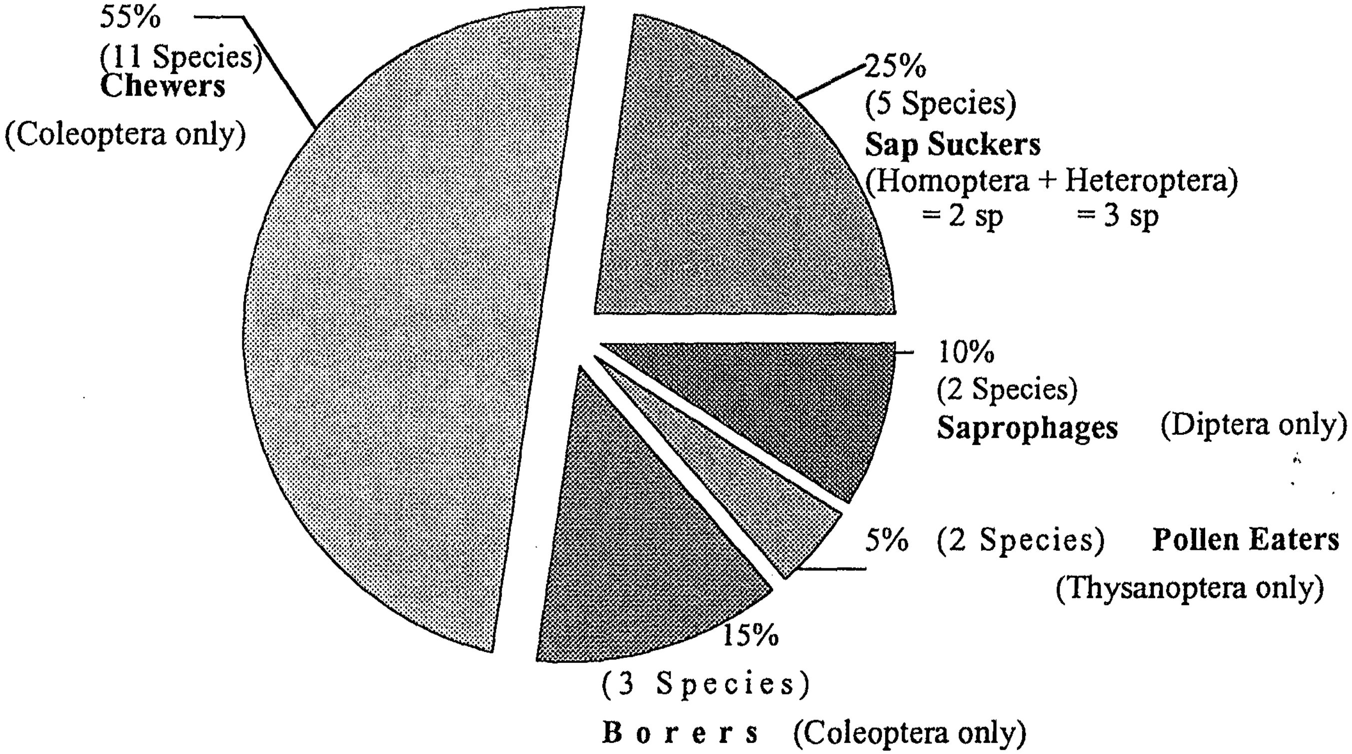


Fig. 6. The percentage of herbivorous insect species of each feeding guild that were found upon *S. pterophorus*. The number of insect species in each feeding guild is placed in parentheses. 22 herbivorous insect species were found upon *S. pterophorus* in total.

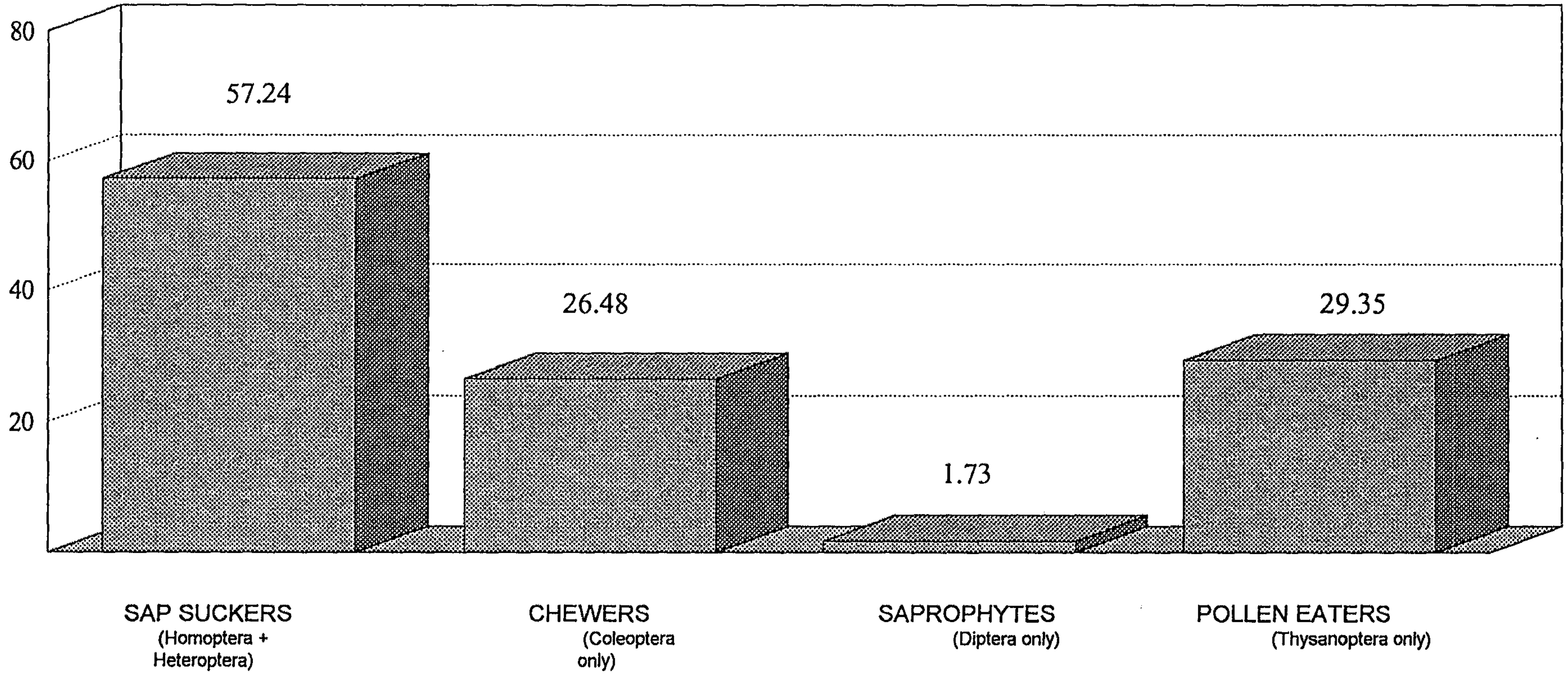


Fig. 7 . **The number of insects/100g dry mass of *S. inaequidens'* in each feeding guild. 4 Guilds were identified.**

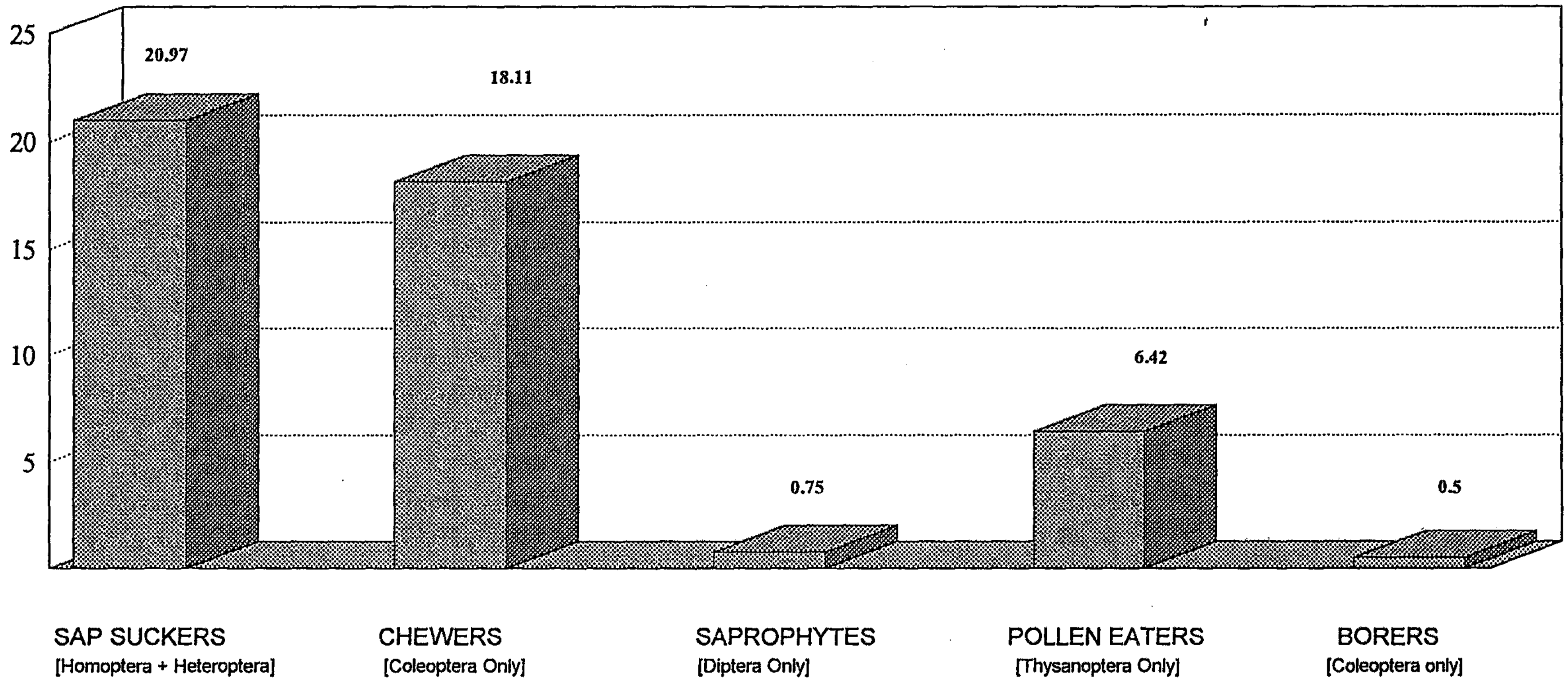


Fig. 8. The number of insects/100g dry mass of *S. pterophorus* in each feeding guild. 5 Guilds were identified

TABLE 5. Total number of insects per 100dry mass of each respective part of plant. Both Sites, A and F,and all the four seasons are represented.

Part of Plant	Number of insects per 100g dry mass.	
	S. pterophorus	*S. inaequidens*
Flowers	518,5	984,4
Foliage	3,7	55,7
Stems	0,6	39,9
Roots	18,3	214,1
The Whole Plant	3,9	81,98
Standard Error	127,8	223,8

Considering the different plant parts as variables, there was a considerable difference in the number of insects per 100g dry mass of host between the two plant species with *S. inaequideus* having more on all parts. On both plant species flowers recruited sap suckers, borers or miners, chewers and saprophages, while stems and roots hosted sap suckers. The foliage of both plant species had sap suckers and chewers. (Stem borers were not found in *S. inaequidens.)*

The number of insect herbivores was significantly different between the parts of the plant for the two plant species ($\chi^2 = 1448.36$ and $\chi^2 = 1857.36, p < 5\%$, for *S. pterophorus* and *S. inaequidens* respectively). Flowers hosted the highest number of insect herbivores, followed by the roots, the foliage and the stems for both plant species considering that they are subterranean, roots would not be expected to come into the second position after flowers, especially with just one insect species.

4.3 BIOLOGICAL OBSERVATIONS ON SOME INSECT HERBIVORES

Thysanoptera

Thysanoptera were found in flowers and there were more on *S. inaequidens* (462,0 insects / 100g dry mass of flowers) than on *S. pterophorus* (177,3 insects / 100g dry mass of flowers). All stages of the thrips were present throughout the sampling period on both plant species. They fed on pollen grains and bred in florets. Adults inserted the whole abdomen into the florets, very likely laying eggs. Infested florets became darkened and finally black. Thrips were found moving about at any time of the day or night, their wings often covered with pollen. None of them was seen actively flying as stated by DALY *ET AL.* (1978), but they were seen floating in the air. It is likely that their mode of dispersal was by wind currents just like the seeds of their hosts. This could be of great advantage in that they could be moved into the same direction as their prospective hosts.

Heteroptera

All of the species in this group caused serious damage to the two plant species. *Nysius* sp. (ACRH 605) and *Spilostethus* sp. (ACRH 435) (both Lygaeidae) caused wilting and dieback of shoots and flowers. *Spilostethus* sp. seemed to be attacking *Senecio* species only while *Nysius* sp. was seen on many plant species. All stages of both insect species were found.

The other Heteroptera that seriously affected the two plant species were *Anoplocnemis curvipes* F. (ACRH 591) and *Cletus* sp. (ACRH 589) (both Coreidae) which fed upon the sap of stems causing dieback of the shoots of which stem they were feeding upon. They were often found in large groups giving the impression that the earlier instars had stayed together. They were found on only the softer parts of the stems of *S. inaequidens* which could bend under the strain of their group weight.

Homoptera

This group was represented by large numbers of each of the two species, the aphids (ACRH 442) and *Hilda patruelis* Stal (ACRH 584) (Aphididae and Tettigometridae respectively). Aphids fed upon the sap of flowers, the foliage and softer parts of stems while *H. patruelis* Stal fed upon lower parts of stems and roots of both plant species. All stages of their life cycle were present throughout the year on the parts mentioned above of both plant species. Both insect species were being attended by Hymenopterous insects.

Coleoptera

Most members of this Order were found on the two *Senecio* species and were common on the other surrounding plant species. (Chapter 3).

Monolepta sp. (ACRH 432) (Chrysomelidae, Galerucinae) was seen on the flowers and foliage of the two plant species but was totally lacking on other plant species in the vicinity. So it is probable that this species was specific at least to the two *Senecio* species, especially *S. pterophorus* to which it caused defoliation to the extent of killing off the plant. It appeared in very large populations but could easily be dislodged by heavy rain and many drowned in the resulting puddles. *Monolepta* sp. chewed the whole tissue but regurgitated the cellulose skeleton. Mating was observed on the plant but it probably laid eggs in the soil since none were found.

The beetles, ACRH 434 and ACRH 594, both Phalacridae, fed upon flowers of the two plant species in which they most likely completed their life cycle since both larvae and adults were found. The smaller beetle, ACRH 434 was the more common of the two. Larvae of both insect species seem to have been responsible for tunnelling through the flowers which, as a result, became yellowish and stunted before drying out eventually.

Cerostis capensis L. (Meloidae) (ACRH 593) adults were found on, and fed upon, flowers of *Senecio* species and other plant species in the vicinity.

The beetle, *Oulema bilineata* Germar (ACRH 597) was a generalist that was found on the flowers and foliage of *S. inaequidens.* It ate all plant tissues and appeared during summer only in large numbers. Only adults were found.

Diptera

Of underestimated importance perhaps were *Trupanea incisa* Munro(ACRH 599) and two yet to be identified, ACRH 958 (Drosophilidae) and ACRH 583 (Chloropidae), whose eggs and larvae could be found among decaying ovaries in the flowers. They could be obtained in numbers by placing flowers in the emergence sleeves. Numbers emerged at a time which implied that the eggs were laid in large numbers in the same flower heads at once. It is likely that the two pteromalid wasps (ACRH 601 & 604) were attacking one or more of the Diptera species.

4.4 PREDATORS AND PARASITOIDS WHICH WERE FOUND ASSOCIATED WITH THE TWO PLANT SPECIES.

There were two predator insect species, *Chilomenes lunata* Fabricius and *Exochomus* sp. (both Coccinelidae - Coleoptera) found on the two plant species. The pteromalid wasps mentioned above (4.3) were found often on the flowers of both plant species. Other wasps of the Family Ichneumonidae were found to parasitise one borer species of *S. pterophorus*. These parasitoids, found at both Site A and Site F, are dealt with in Chapter 6 in more detail.

4.5 DISCUSSION

Some of the insect species collected from *S. pterophorus* and *S. inaequidens* might be of some economic importance, but in many cases the exact species still need to be verified. This fact should not imply that the two plant species merit serious consideration as important alternative hosts for agriculturally important pests since many of the phytophages were generalists.

Thrips are agriculturally important. Troublesome species were reported to alternate between onions and *Senecio* species (KRANZ *ET AL.*, 1978). The "false chinch bug", *Nysius natalensis* Evans, (ACRH 605) is thought to be indigenous to South Africa and known as a pest of wheat, oats, barley, rye, sunflowers, pastures and fodder crops. (ANNECKE AND MORAN, 1982). Similarly the *Spilostethus* species (ACRH 435) found on the two *Senecio* species could be the same as the "seed bugs" which attack the seeds of sunflower (ANNECKE AND MORAN, 1982).

Anoplocnemis curvipes F. (ACRH 591) is a generalist reported on many crops in South Africa (ANNECKE AND MORAN, 1982), such as granadillas, beans, beetroot, carrots, pepper, lettuce, peaches, sweet potatoes and the whole family of Curcubitaceae. It is claimed that it has been recorded on over 100 species of plants belonging to 38 families. A second generalist pest is *Hilda patruelis* Stal, (ACRH 584) commonly know as the "tea bug" and reported feeding upon tea, ground nuts, legumes, sunflower, maize, citrus and ornamental trees. (ANNECKE AND MORAN, 1982).

Oulema bilineata Germar (ACRH 597), commonly known as "gooseberry beetle", and its larvae, know as the "tobacco slug", feeds upon *Nicotiana glanca* L. (or wild tobacco), gooseberries and potatoes. It is also a pest of a serious weed, *Datura stramonium* L. which is common in South Africa. (ANNECKE AND MORAN, 1982). KALULE - SABIITI (1991) thought that *Decapotoma* sp. (ACRH 593) was the one that ate legume flowers around Umtata.

Astylus atromaculatus Blanchard (Melyridae) (ACRH 595) is commonly known as "spotted maize beetle". Its larva was reported to feed upon maize seeds before and after germination while adults consume flowers of legumes, ornamentals and green pepper (ANNECKE AND MORAN, 1982). KALULE - SABIITI (1991) confirmed that adults ate legume flowers but said that its larva was the more serious pest that fed upon embryos inside maize cobs.

More differences than similarities between the two plant species were illustrated by the numbers of individual insects and kind of insect species that were recorded on the different parts of the plant species.

S. pterophorus was the larger plant species with a wider pith lumen and a higher population density (Table 1) that could accommodate the larvae of three borer species, *Lixus* sp. (ACRH 581), a species of Cerambycidae, and the smallest of the three borer species, *Mordella* sp. (ACRH 580). The larger surface area and volume could have created more niches to accommodate a larger number of insect species (LAWTON AND SHROEDER, 1977). *S. pterophorus*, in spite of the greater mass of the stems had harder stems, provided relatively fewer opportunities to sap suckers unlike *S. inaequidens* which recruited two more insect species from this guild.

S. pterophorus had, it appears, more defences such as the poisonous alkaloids (Chapter 1, page 2) and the trichomes on the leaves (Chapter 3, section 3.2). Under the microscope the trichomes were seen to be quite long and fairly dense. Four options seemed to be available for insects to exploit that kind of leaf.

a) Larger insects with large mandibles could ignore the trichomes,
b) the possession of a long proboscis would enable the insect to reach the leaf surface,
c) tiny insects could fit between the trichomes or,
d) access to food could be achieved by mowing down the trichomes before feeding.

Three of those strategies were found amongst the herbivores of *S. pterophorus*;

a) *Monolepta* sp. (ACRH 432) had large enough mandibles to chew trichomes and leaf together,

b) *Spilostethus* sp. (ACRH 435) had long enough mouth parts to reach the surface of the leaf; and

c) Aphids (ACRH 442) were small enough to move between the trichomes to gain access to the leaf surface.

The protective nature of alkaloids of *S. pterophorus* was highlighted by the fewer number of shared insect herbivores while the longer life span of *S. pterophorus* increased its suitability to additional overwintering endophages with longer life cycles such as *Lixus* sp.

Results in Table 3 (page 33) support the idea that plant taxonomic relatedness can be proved by the sharing of herbivorous insect species (HODKINSON AND HUGHES, 1982). Parts of *S. pterophorous* which anatomically resemble those of *S. inaequidens*, the roots and flowers, shared more insect species than parts with little resemblance, the stems and foliage. This idea implies that polyphagous insects seek and identify characteristics (structures, colours or chemicals) required for their survival rather than a particular plant species. Utilising a range of plant species is inevitable because such sought after characteristics are likely to be continous variables, within a mixed population of closely related species like *Senecio* and also over a period of time. More specific ones, like the borer species, must however be guided by distinct or combinations of unique characteristics of their host such as the trichomes of the foliage and the toxic alkaloids of *S. pterophorus*. Apparently *S. inaequidens* features no unique characteristics and so recruited no specific herbivores.

5 SEASONAL OCCURRENCE OF HERBIVOROUS INSECTS ON *S. pterophorus* and *S. inaequidens*

5.1 INTRODUCTION

Studies of the seasonality of insect herbivores in relation to their hosts is useful in evaluating the seriousness of some of the insect herbivores and is necessary in identifying candidates for biocontrol (HARRIS ; 1973) , if such a measure may be required in future for controlling *S. pterophorus* and *S. inaequidens*.

An attempt was made to investigate the seasonality of insect phytophages and their two host species and correlation coefficients, r_s, were used to find out whether there was any relationship between the seasonality of insect phytophages and seasonality of their hosts. Other potential population regulation factors such as the number of predators, availability of oviposition sites and weather were kept in mind. Data included all the stages except eggs.

The seasons, winter, spring, summer and autumn were represented by the months of July 1986, October 1986, January 1987 and April 1987 respectively. The temperatures on the days data was collected are given in Table 6.

TABLE 6. Temperature ranges during sampling on the sampling days.

Months	July	October	January	April
Temperature (^{0} C)	18,2 - 23,0	22,1 - 23,2	22,6 - 26,8	20,3 - 24,5

Table 6 above indicates that the temperature ranges were not very different on the days when insects were collected. It should however be noted that these temperatures are not representative of the means for the respective months or seasons. On the other hand that these temperature ranges did not differ considerably between seasons could suggest that significant differences in the number of insect herbivores and the number of their species that may be realised would not be due to temperature . In order to understand the seasonal influence of host plants upon herbivorous insect populations and species an analysis of fluctuations in dry masses of the two plant species was done for both sites, A and F. Tables 7 and 8 below gives the mean dry mass per plant during the four seasons in the two sites. Kruskal Wallis 'H' analysis was used to test for seasonality of the dry mass of plant material.

TABLES 7 and 8. **Mean dry masses per plant over the sampling period (in grams). Each value is a mean of 32 plants of *S. inaequidens* and of 16 plants of *S. pterophorus* per sampling occasion in each site.**

TABLE 7. SITE A

Months	July	October	January	April
S. inaequidens ± Std. Error	9,5 ± 3,1	9,1 ± 2,1	9,6 ± 2,3	9,6 ± 3,1
S. pterophorus ± Std. Error	167,3 ± 42,7	390,7 ± 26,5	378,2 ± 59,7	410,6 ± 38,1

The Kruskal - Wallis test showed no significant seasonality for *S. inaequidens* *(H = 0,02; p>95%)* but a significant seasonal variation for *S. pterophorus (H = 19,8; p<5%)* at Site A. The mean dry mass per plant of *S. pterophorus* was highest during the warmer months (October, January and April) but low during the winter month of July.

TABLE 8. SITE F

Months	July	October	January	April
S. inaequidens ± Std. Error	9,0 ±2,8	9,0 ±3,6	7,9 ± 2,4	9,9 ± 4,0
S. pterophorus ± Std. Error	81,2 ±36,3	216,0 ±44,5	238,9 ±31,6	285,8 ±47,7

Mean dry mass was significantly different at Site F for *S. pterophorus* (*$H = 25{,}00$; $p < 5\%$*) as well as for *S. inaequidens* (*$H = 9{,}44$; $p<5\%$*), between the different seasons. The mean dry mass for *S. pterophorus* was increasing continuously from July up to April having recorded the highest value in April as was the case at Site A. Similarly, the mean dry mass for *S. inaequidens* was highest during April but lowest during January at Site F. Tables 7 and 8 suggest that *S. pterophorus* plants in the sites that were sampled went on increasing their dry mass during the sampling period - supporting the view stated in Chapter 3 (p. 22) that this plant species could be biennial unlike *S. inaequidens* which is annual.

Correlation coefficient of dry mass between sites during the four seasons was not significant for both plant species. ($r_s = 0{,}8$ for *S. pterophorus* and $r_s = -0{,}2$ for *S. inaequidens*; $p>95\%$). This suggests that the growth or development of the plants in Site A was out of phase with that in Site F. For this reason the results for Site A were analysed separately from the results for Site F.

5.2 SEASONALITY OF, AND RELATIONSHIP BETWEEN DRY MASS OF PART OF THE HOST PLANTS, NUMBERS OF INSECT SPECIES WHICH WERE FOUND UPON EACH OF THE PARTS AND NUMBER OF INSECT HERBIVORES/100 GRAMS OF DRY MASS OF PLANT MATERIAL.

Having found that the dry mass of whole plants of *S. pterophorus* varied seasonally in both sites while that of *S. inaequidens* varied only in Site F, it was necessary to find out which parts of the plant contributed towards that seasonality and thereafter calculate the correlation coefficients, r_S, between the dry mass of such parts of the plant against the number of insect herbivores per 100g dry mass of each respective part of plant material as well as against the number of herbivorous insect species. Also note that the number of insects was expressed against the dry mass of each respective part, thus it was necessary to analyse the seasonality of each of these plant parts separately. A significant correlation would suggest that herbivorous insects influenced the dry mass of their hosts or that the dry mass of plants influenced the number of species and the numbers per 100g dry mass of plant material of herbivorous insects. The number of herbivorous insects are expressed as numbers of insect herbivores per 100g dry mass of appropriate plant parts in Tables 9 up to 17 which also give the corresponding dry masses of the plant parts in each season and site as well as the seasonality of the number of species of insect herbivores. Bar charts were constructed representing these tables followed by bar charts which represent the seasonality of the number of the more important herbivorous insects species upon the different parts of the two plant species in order to give an overall seasonal pattern. In all the bar charts striped bars represent Site A, while blank bars represent Site F. Important insect herbivores were arbitrarily defined as those that occurred in at least three seasonal samples or those which caused death of plant tissues. These herbivorous species which were more polyphagous (i.e. found on many other plant taxa) such as Aphids *H. patruelis*, and *A. versicolor* and the beetles ACRH 434 and ACRH 594 (both cryptocephaline) were not included among the important insect species although they appeared during all four seasons and caused visible damage.

The Kruskal - Wallis analysis "H" was calculated to test for any seasonal variation of the dry mass of plant parts as well as the number of insect herbivores while the Chi-Squared test was employed to test for seasonality in the number of herbivorous insect species. A significant seasonality in either case would suggest that "seasons" affected the attribute in that case while a non-significant one would not explain the effect of seasons.

Note that correlations were calculated only when the dry mass of the appropriate plant part had been found to be significantly seasonal. A 95% level of confidence was used in all cases.

5.2.1 SEASONALITY OF INSECT HERBIVORES UPON FLOWERS.

Tables 9 and 10 below show the seasonal variation of the dry mass of flowers per plant, the number of insect herbivores of flowers and the number of herbivorous insect species of *S. pterophorus and* S. *inaequidens* respectively, at Sites A and F.

TABLE 9. Seasonality of insect herbivores upon flowers and dry mass of flowers of *S. pterophorus.*

TABLE 9(a) SITE A

Month	July	October	January	April	Analysis
Dry mass of flowers / plants (±Std. Error)(g)	0,18 ± 0,03	1,87 ± 0,34	2,70 ± 0,43	0,12 ± 0,02	H = 44,25
No. of insect herbivores/100g dry mass of flowers (± Std. Error)	1142,86 ± 820,89	247,99 ± 57,45	316,84 ± 63,76	4840,43 ± 1366,72	H = 5,96
No. of herbivorous insect sp.	3	11	12	6	Chi^2 =6,24

From Table 9(a), seasonal variation was found to be significant for the dry mass of flowers (H=44,25; p<5%) but not for numbers of insect herbivores (H = 5,96; p>95%). The correlation coefficient r_s, between dry mass of flowers and number of insect herbivores of flowers was -0,08, and between dry mass of flowers and number of species of insect herbivores was +0,8, thus both correlations were not significant (p>95%; Table 9(a)). This suggests that the recruitment of insect herbivores of flowers was not directly influenced by the dry mass of flowers at Site A. The Chi-squared test showed no seasonality in the number of herbivorous insect species either (Chi^2 = 6,24; p>95%), although there is an apparent increase of insect species during October and January, which corresponds well with the higher dry mass of flowers during these same months contrary to the nonsignificance of the correlation coefficient between the two aspects. Therefore there was no significant relationship between the herbivorous insects of flowers and the dry mass of flowers at Site A.

TABLE 9(b) SITE F

Month	July	October	January	April	Analysis
Dry mass of flowers / plants (±Std. Error)(g)	0,08 ± 0,01	1,04 ± 0,33	1,71 ± 0,23	0,14 ± 0,02	H = 48,48
No. of insect herbivores/100g dry mass of flowers (± Std. Error)	1259,26 ± 351,46	372,60 ± 117,63	421,25 ± 114,44	2626,73 ± 694,26	H = 10,08
No. of herbivorous insect sp.	4	9	10	5	Chi^2 =2,68

The dry mass of flowers and the number of insect herbivores upon flowers of *S. pterophorus* at Site F were significantly seasonal (H = 48,48 and H =

10,08, respectively; p<5%). While the dry mass of flowers was higher during October and January, the number of insect herbivores were lowest during these two months. Although the number of herbivorous insect species was not significantly seasonal (Chi^2 =2,68; p>95%), higher numbers were recorded during October and January and correspond to the higher dry mass of flowers during the same months such that the seasonality of the dry mass of flowers and number of species of insect herbivores was perfectly and positively correlated (r = +1,00) [Fig 9]. The increase in the dry mass of flowers could have influenced the increase in the number of species of insect herbivores. The correlation coefficient between the number of insect herbivores and the dry mass of flowers was however not significant (r=0,8; p>95%) thus the seasonality of the dry mass of flowers was independent of the number of insect herbivores. Note that flowers were significantly more during October and January in both sites. This data agrees with earlier observations of the flowering patterns of *S. pterophorus* for October but not for April (Chapter 3 page 25). The difference between this data and earlier observations was probably due to differences in climate during the two periods when observations and data were taken and could be showing the sensitivity of flowering of *S. pterophorus* towards climate rather than towards seasons or times of year as indicated in Chapter 2 and Chapter 3. The flower herbivores of *S. pterophorus* have to be adapted to this kind of uncertainty such that their number of species may not be significantly seasonal and the herbivores had to be generalists.

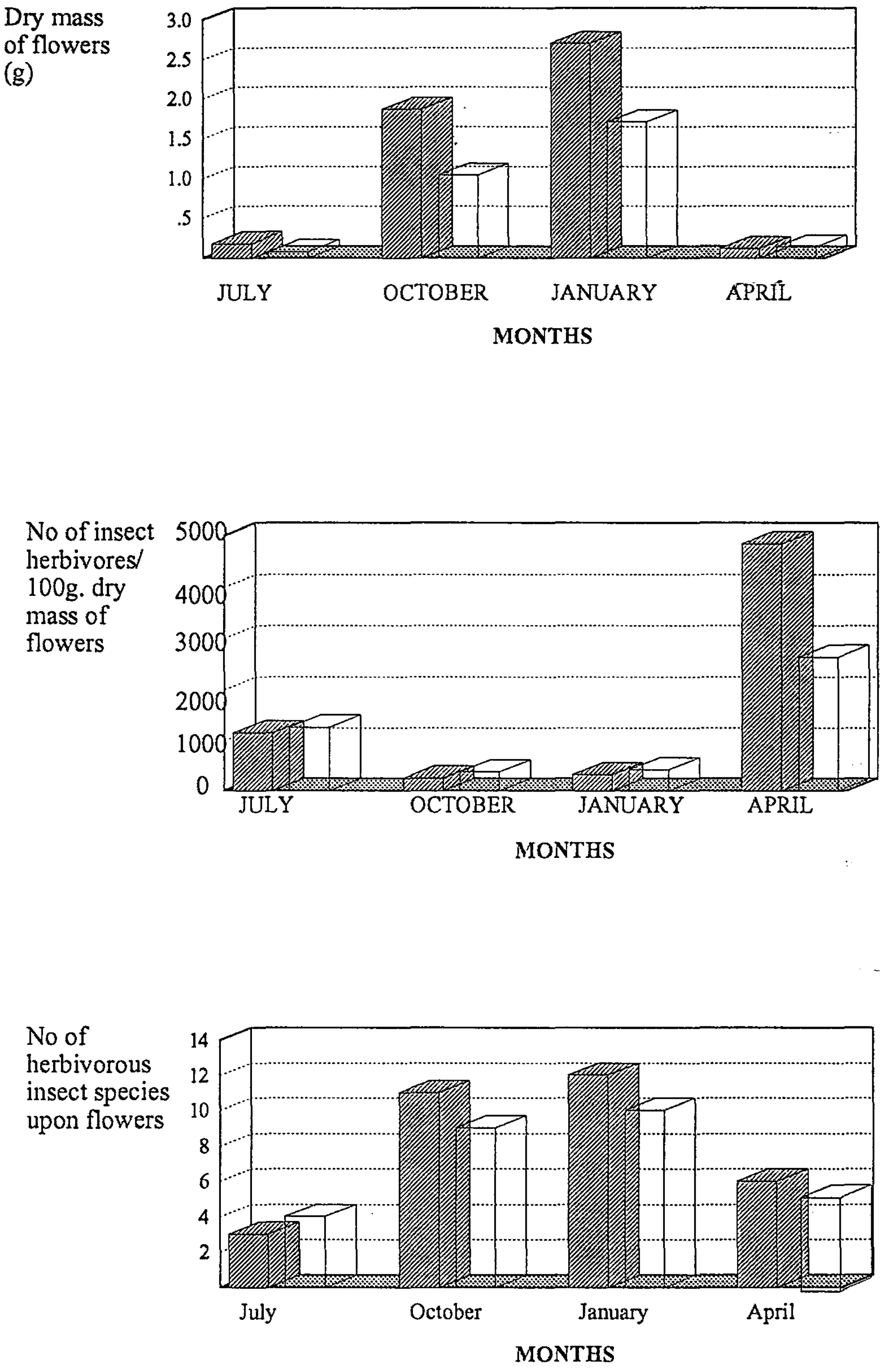


Fig. 9. **The seasonality of the number of insect herbivores, number of herbivorous insect species and the dry mass of flowers of *S. pterophorus*.**

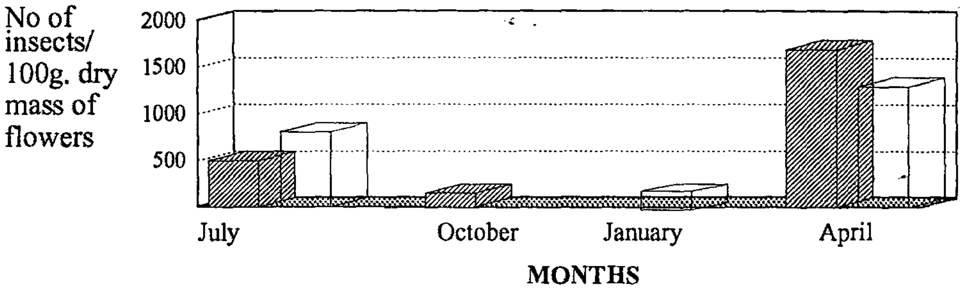


Fig. 10. **Thrips on the flowers of *S. pterophorus.***

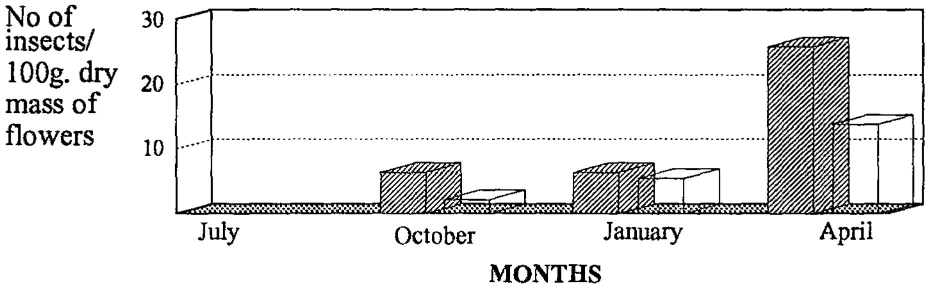


Fig. 11. **Seasonal occurence of *Nysius* sp. on the flowers of *S. pterophorus.***

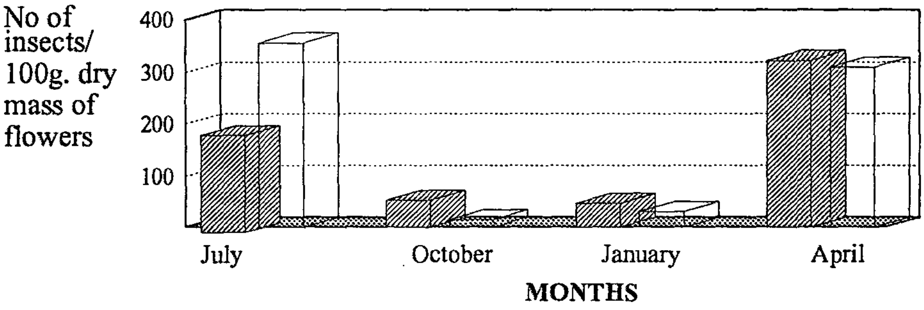


Fig. 12. ***Spilostethus* sp. on the flowers of *S. pterophorus.***

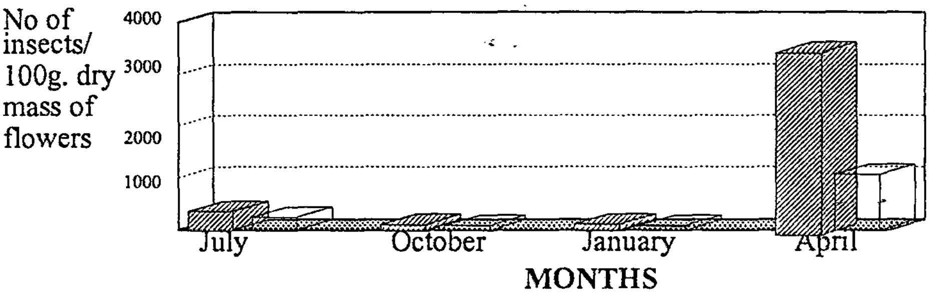


Fig. 13. **Beetle ACRH 434 on the flowers of *S. pterophorus*.**

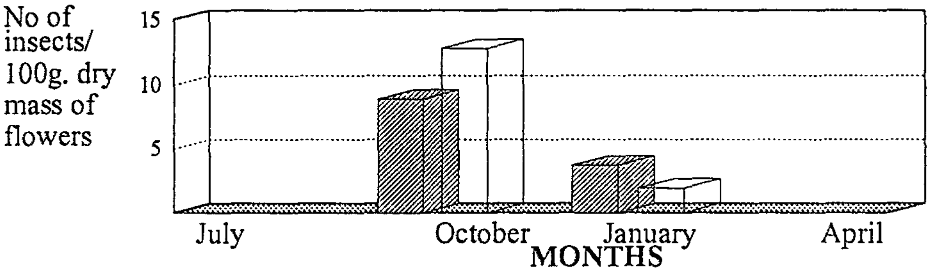


Fig. 14. ***Monolepta* sp. on the flowers of *S. pterophorus***

Figs. 10 to 14 show the seasonality of the more important insect herbivores that were collected from the flowers of *S. pterophorus*. With the exception of *Monolepta* sp. other flower herbivores in Figs. 10 to 13 showed high numbers during April. This high figure is also reflected in Fig. 9.

TABLE 10 Seasonality of insect herbivores upon flowers and dry mass of flowers of *S. inaequidens.*

TABLE 10(a) SITE A

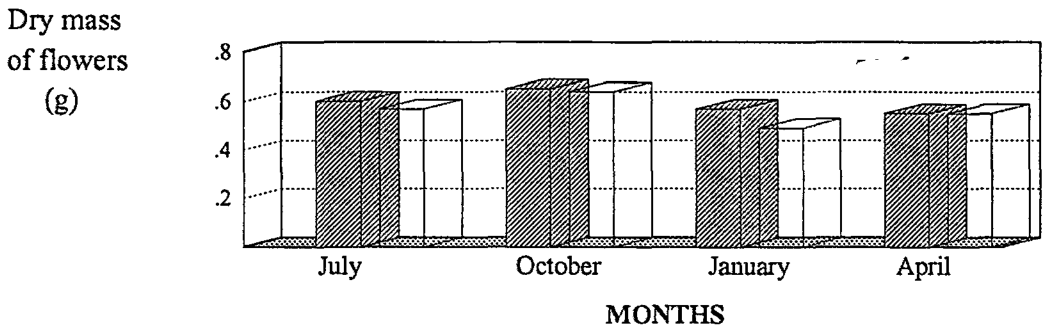
Month	July	October	January	April	Analysis
Dry mass of flowers / plants (±Std. Error)(g)	0,60 ± 0,14	0,65 ±0,15	0,57 ± 0,12	0,55 ± 0,17	H = 3,38
No. of insect herbivores/100g dry mass of flowers (± Std. Error)	524,15 ± 362,04	1888,78 ± 312,72	1210,79 ± 159,81	757,93 ± 128,16	H = 6,51
No. of herbivorous insect sp.	5	8	9	4	Chi^2 =2,94

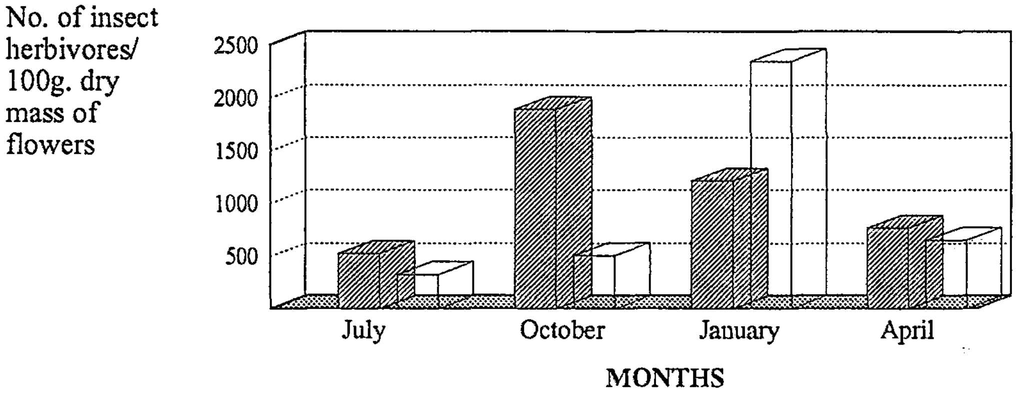
There was no aspect that was significantly seasonal at Site A with regard to flowers of *S. inaequidens*. (Table 10(a); p>95% or H=3,38, H=6,51 and Chi^2 =2,94).

TABLE 10(b) SITE F

Month	July	October	January	April	Analysis
Dry mass of flowers / plants (±Std. Error)(g)	0,57 ± 0,18	0,64 ± 0,23	0,49 ± 0,15	0,55 ± 0,24	H = 7,43
No. of insect herbivores/100g dry mass of flowers (± Std. Error)	326,26 ± 0,37	505,35 ± 0,06	2343,65 ± 0,05	653,89 ± 0,05	H = 17,63
No. of herbivorous insect sp.	6	8	9	4	Chi^2 =2,19

In Table 10(b) above, the number of insect herbivores was significantly seasonal (H = 17,63; p<5%) but not the number of their species (Chi^2 =2,19; p>95%). The dry mass of flowers was also not seasonal (H = 7,43; p>95%). It is also shown that the Standard Errors of the number of insect herbivores during each of the seasons in Table 10(b) was much lower than those in Table 10(a). (i.e. Site F Standard Errors lower than those at Site A.) This suggests that the distribution of insect herbivores on flowers on each plant during each of the seasons at Site F was more uniform than that at Site A. The high numbers of insect herbivores, upon the flowers of *S. inaequidens* during the warm month is well illustrated in Fig. 15. The dry mass of flowers of *S. inaequidens* did not fluctuate much seasonally (Fig. 15). This uniformity was in line with the observation that *S. inaequidens* flowered, not according to seasons, but by availability of moisture (Chapter 3, page 25) and there was rain, fog or frost any time of the year (Chapter 2, page 6).





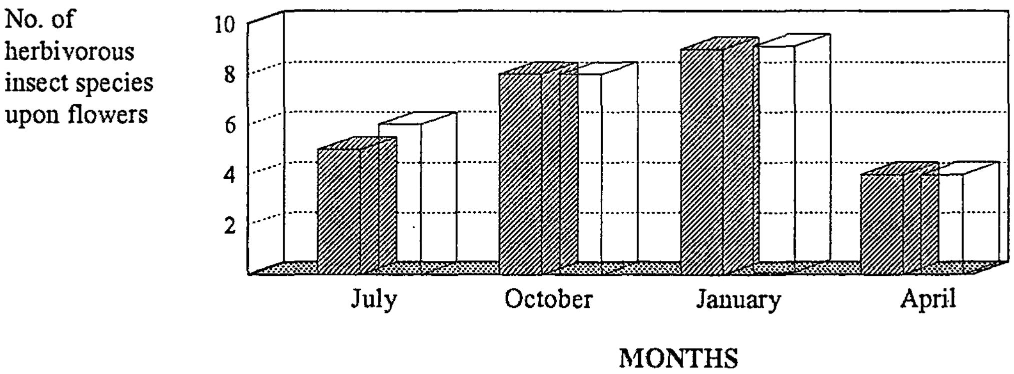


Fig. 15. **Seasonality of the dry mass and insect herbivores of flowers of *S. inaequidens* (all insect species included).**

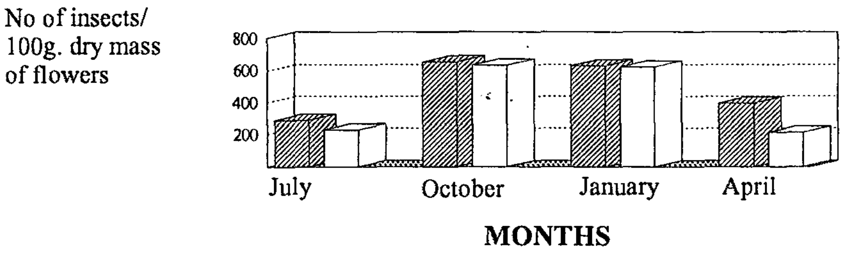


Fig. 16. **Seasonal occurence of thrips (*Thripidae*). on the flowers of *S. inaequidens*.**

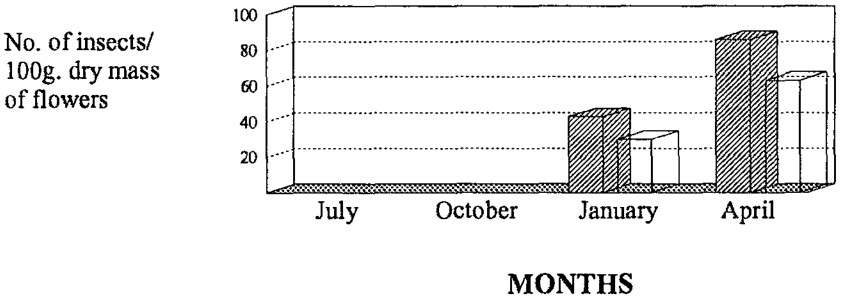


Fig. 17 . ***Nysius* sp.on the flowers of *S. inaequidens***

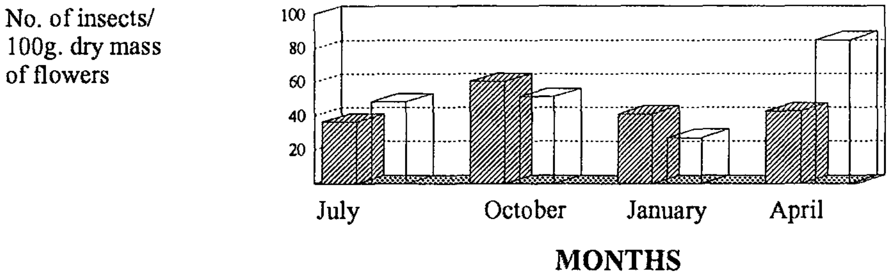


Fig. 18. **Seasonal occurence of *Spilostethus* sp. on the flowers of *S. inaequidens*.**

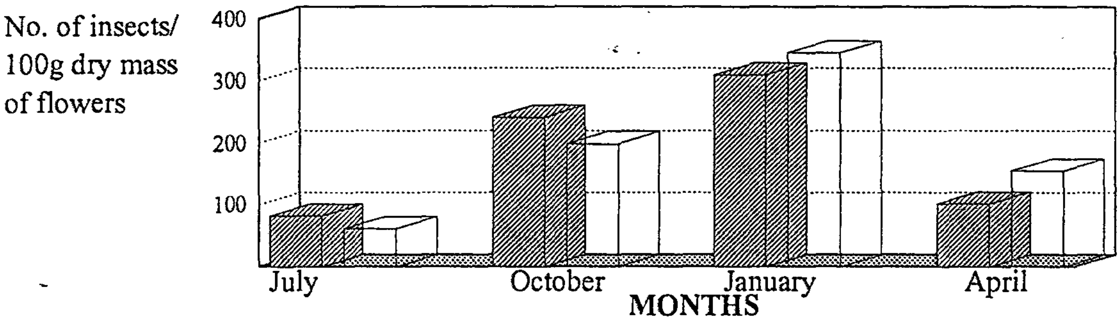


Fig. 19. **Seasonal occurence of Beetle ACRH 434 on the flowers of *S. inaequidens***

With the exception of *Nysius* sp. the other three flower herbivores upon *S. inaequidens* appeared throughout the sampling period in both sites. (Figs. 16, 19). The patterns of the 'important' flower insects which appeared on both plant species have no similarity (Figs. 10 - 14 and Figs. 16 - 19).

Important insect herbivores were more numerous during April on the flowers of *S. pterophorus* while on the flowers of *S. inaequidens* their number was highest during January. The reasons for this difference are not clear, but it is likely that the insects upon the flowers of *S. inaequidens* responded to the summer season while insects upon the flowers of *S. pterophorus* responded to some, still obscure, characteristics of the flowers of *S. pterophorus* during April. However, with reference to Tables 9(a) and 9(b) the dry mass of the flowers of *S.pterophorus* decreased during April in both sites while Tables 10(a) and 10(b) show that the dry mass of the flowers of *S. inaequidens* remained about the same in both sites. Mathematically, if the population of flower insect herbivores remained the same during April, accompanied by a drop in the dry mass of the flowers of *S. pterophorus* or if the numbers of insects decreased but at a lesser extent than the flowers did then the number of insects / 100g dry mass of flowers would increase. That is, an increase in the number of insects / 100g dry mass does not necessarily represent an increase in the population of insect herbivores and vice versa. This view needs to be kept in mind when analysing data of the other plant parts.

5.2.2 SEASONALITY OF INSECT HERBIVORES UPON THE FOLIAGE.

Tables 12 and 13 and Figs. 20 to 26 below show the seasonal variation of the dry mass of foliage per plant, the number of insect herbivores of foliage and the number of species of insect herbivores on the foliage of *S. pterophorus* and *S. inaequidens* respectively at Sites A and F.

TABLE 11 Seasonality of insect herbivores and dry mass of the foliage of *S. pterophorus*.

TABLE 11(a) SITE A

Month	July	October	January	April	Analysis
Dry mass of foliage/ plants (±Std. Error)(g)	43,64 ± 12,13	110,57 ± 7,48	91,67 ± 14,48	73,68 ± 6,84	H = 20,04
No. of insect herbivores/100g dry mass of foliage (± Std. Error)	1,00 ± 0,48	5,31 ± 1,28	4,09 ± 1,56	3,56 ± 1,00	H = 8,51
No. of herbivorous insect sp.	4	8	7	6	Chi^2 =1,40

Table 11(a) shows that seasonality of the dry mass of the foliage/plant was significant (H = 20,04; p<5%), as well as the number of insect herbivores upon the foliage of *S. pterophorus* (H = 8,51; p<5%) but not the number of herbivorous insect species (Chi^2 =1,40; p>95%). Therefore the number of insect herbivores was highest during October, but decreased towards January on to April. The seasonal trend corresponds perfectly with that of the dry mass of foliage such that the seasonal correlation coefficient r_s was, surprisingly, equal to +1,00. Fig. 23 shows this. This correlation suggests a strong influence of the dry mass of the foliage upon the recruitment of insect herbivores or vice versa.

TABLE 11(b) SITE F

Month	July	October	January	April	Analysis
Dry mass of foliage / plants (±Std. Error)(g)	21,18 ± 9,51	61,38 ± 12,58	57,91 ± 7,65	51,28 ± 8,56	H = 24,22
No. of insect herbivores/100g dry mass of foliage (± Std. Error)	0,89 ± 16,63	2,95 ± 4,38	5,29 ± 6,96	2,68 ± 2,92	H = 3,99
No. of herbivorous insect sp.	2	8	8	5	Chi^2 =4,05

Table 11(b) shows that unlike Site A it was the seasonality of the dry mass of the foliage that was significant (H = 24,22; p<5%), but not the number of insect herbivores (H = 3,99; p>95%), or the number of herbivorous insect species (Chi^2 = 4,05; p>95%). The highest dry mass was recorded during October, but decreased onto January and April. Aspects in Table 11(b) above were not significantly correlated (r = 0,80 between dry mass of foliage and number of insect herbivores and r = 0,95 between the dry mass of foliage and number of herbivorous insect species; p>95%).

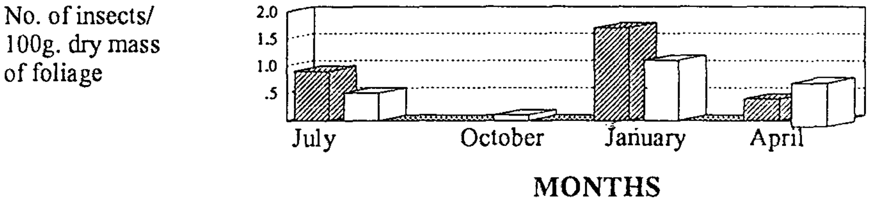


Fig 20 *Nysius* sp. on the foliage of *S. pterophorus.*

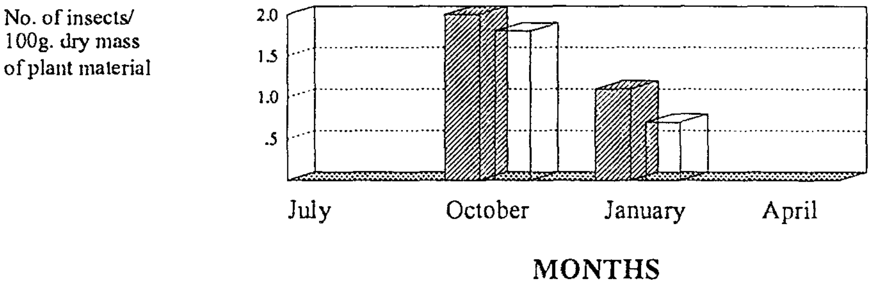


Fig. 21 *Monolepta* sp. on the foliage of *S. pterophorus*

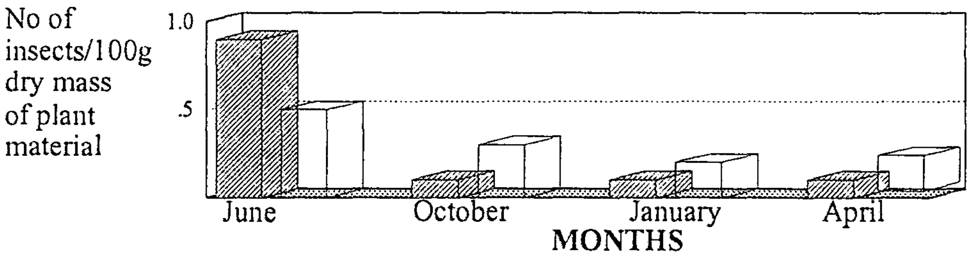


Fig. 22 *Spilosethus* sp. on the foliage of *S. pterophorus*

All the three herbivorous species in Figs. 20, 21 and 22 caused serious damage and often death to foliage tissue, especially the shoots of *S. pterophorus*. The seasonal pattern of *Nysius* sp. (Fig. 20) and that of *Spilostethus* sp. (Fig. 22) contradicted the overall patterns of all the insect herbivores together (Fig. 23). Therefore the other foliage insect herbivores were relatively much more than these two important insect species. These two insect species seem to have been adapted to exist during Winter when the majority of the other foliage insect herbivorous species were absent. This strategy allowed them to feed with reduced competition. *Monolepta* sp. were drastically reduced as a result of being easily dislodged by rain from their hosts and being carried away or drowned in the puddles that resulted.

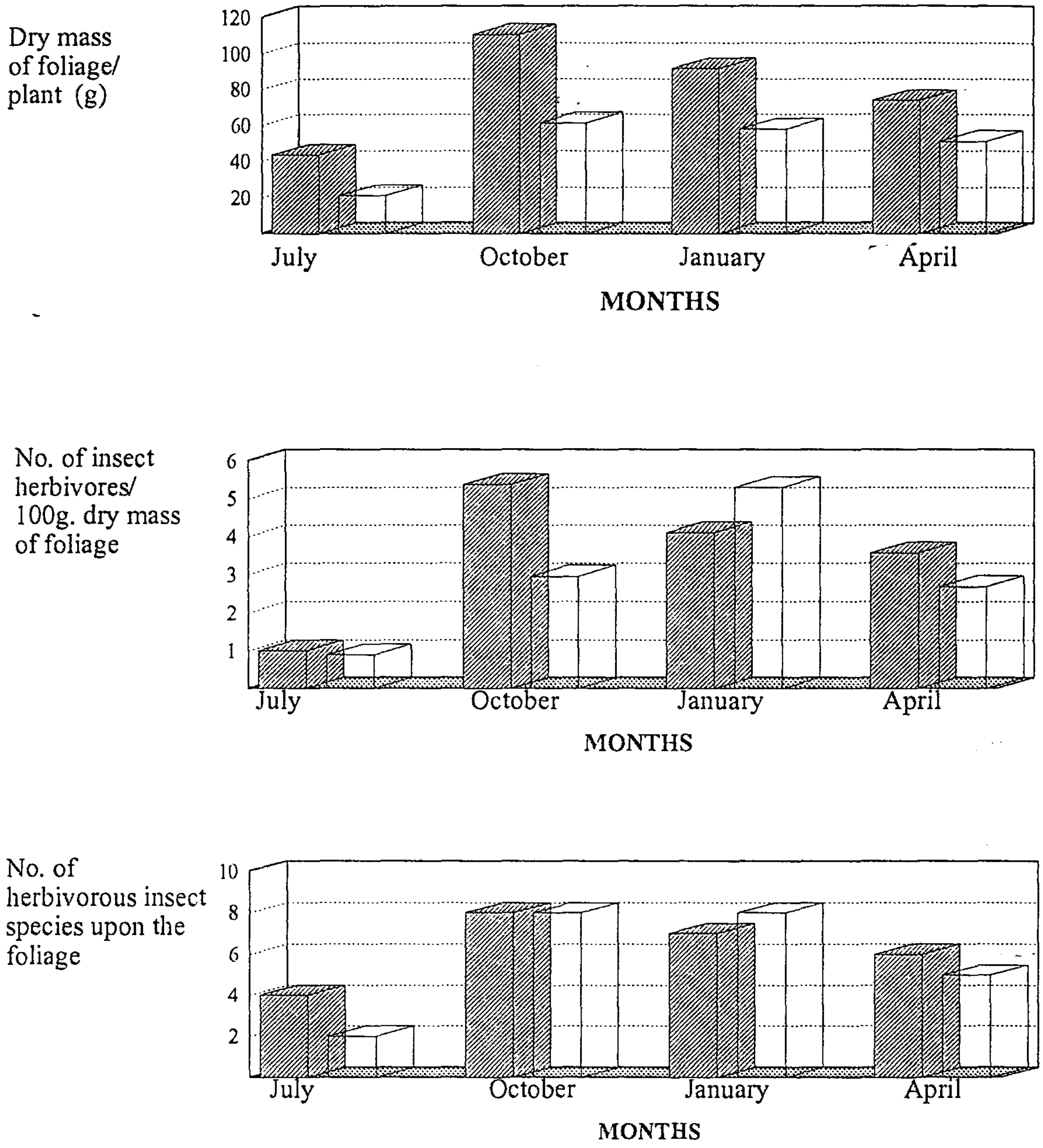


Fig. 23. **The seasonality of insect herbivores and dry mass of the foliage of *S. pterophorus* (all insect herbivores included).**

As with flowers there was no evidence of insect herbivores affecting the dry mass of the foliage of *S. pterophorus*.

TABLE 12 Seasonality of insect herbivores and dry mass of the foliage of *S. inaequidens*

TABLE 12(a) SITE A

Month	July	October	January	April	Analysis
Dry mass of foliage / plants (±Std. Error)(g)	2,07 ± 0,57	2,38 ± 0,41	2,13 ± 0,49	2,19 ± 0,72	H = 6,54
No. of insect herbivores/100g dry mass of foliage (± Std. Error)	27,11 ± 5,84	128,52 ± 21,40	164,05 ± 40,64	121,08 ± 24,78	H = -5,64
No. of herbivorous insect sp.	3	6	8	6	Chi^2 =2,22

None of the dry mass of foliage / plant, number of insect herbivores of foliage or number of herbivorous insect species was significantly seasonal (H = 6,54; H = 5,64 and Chi^2 = 2,22 respectively; p>95%), and so the dry mass of plants may have, or not have affected the recruitment of insect herbivores.

TABLE 12(b) SITE F

Month	July	October	January	April	Analysis
Dry mass of foliage / plants (±Std. Error)(g)	2,51 ± 0,71	2,35 ± 0,92	1,75 ± 0,66	2,24 ± 0,98	H = 10,85
No. of insect herbivores/100g dry mass of foliage (± Std. Error)	11,18 ± 16,21	87,82 ± 24,40	87,69 ± 20,77	66,53 ± 12,15	H = -16,19
No. of herbivorous insect sp.	4	6	8	6	Chi^2 =1,33

Table 12(b) shows that the number of insect herbivores as well as the dry mass of foliage were significantly seasonal (H = 16,19 and H = 10,85 respectively; p<5%;) while the number of herbivorous insect species were not (Chi^2 = 1,33). More insect herbivores were found during October and January, with the winter month of July scoring the lowest, while the mass of the foliage decreased from July up to January.

Table 13(a) also gave the following correlation coefficients; between the dry mass of foliage and number of insect herbivores r_S = -0,30, between the number of insect herbivores and number of herbivorous insect species,

r_S= +0,65 and between number of herbivorous insect species and dry mass of foliage r_S = -0,85. None of the above correlation coefficients was significant, (p>95%). The dry mass of foliage did not seem to affect the number of insect herbivores upon them.

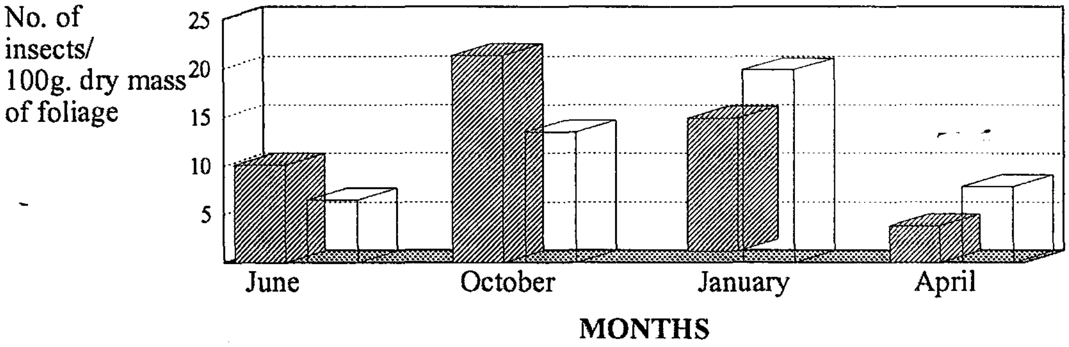


Fig. 24 ***Spilostethus*** **sp. on the foliage of** ***S. inaequidens.***

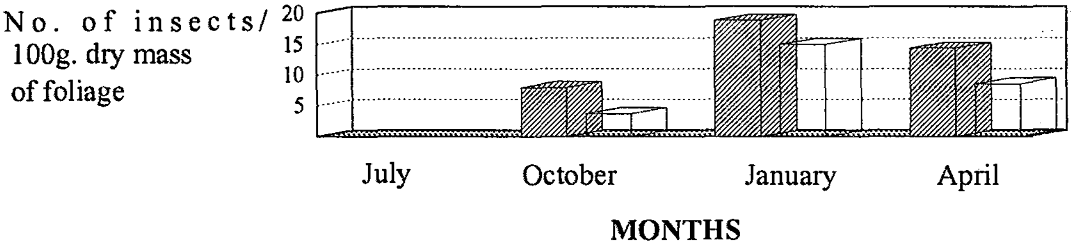


Fig. 25 ***Nysius*** **sp. on the foliage of** ***S. inaequidens.***

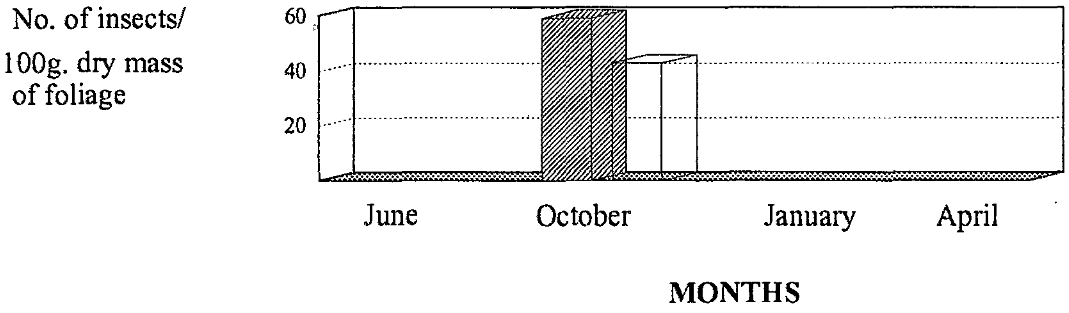


Fig. 26 ***Monolepta*** **sp. on the foliage of** ***S. inaequidens.***

The seasonality of *Spilostethus* sp. upon the foliage of *S. inaequidens* (Fig. 24) was somehow out of phase with its seasonality upon the foliage of *S. pterophorus* (Fig. 22) in that it appeared upon *S. inaequidens* during the warmer months. This insect species was also recorded upon *S. inaequidens* throughout the sampling period. *Nysius* sp. which was well represented during winter upon *S. pterophorus* (Fig. 20) was totally absent upon *S. inaequidens* during that period (Fig. 25). That *Monolepta* sp. was a spring or summer insect species was emphasised by its presence upon *S. inaequidens* during October only (Fig. 26).

5.2.3 SEASONALITY OF INSECT HERBIVORES UPON THE STEMS

Tables 13 and 14 show the seasonal variation of the mean of dry mass of the stems per plant, the number of insect herbivores and the number of herbivorous insect species upon stems of *S. pterophorus* and *S. inaequidens* respectively at Site A and Site F.

TABLE 13 Seasonality of insect herbivores and dry mass of the stems of *S. pterophorus*

TABLE 13(a) SITE A

Month	July	October	January	April	Analysis
Dry mass of stems / plants (±Std. Error)(g)	96,37 ± 24,56	245,49 ± 16,63	257,96 ± 40,73	308,08 ± 28,68	H = 24,49
No. of insect herbivores/100g dry mass of stems (± Std. Error)	0,78 ± 0,82	0,18 ± 0,05	0,22 ± 0,07	0,26 ± 0,07	H = -7,27
No. of herbivorous insect sp.	4	4	4	4	Chi^2 =0,00

Table 13(a) shows that the dry mass of stems / plant was significantly seasonal, (H = 24,49) , but not the number of insect herbivores (H = 7,27; p>95%). However, while the number of insect herbivores was unexpectedly highest during July and lowest during October, the dry mass of the stems was continuously increasing from July to April, possibly due to secondary growth. The dry mass of stems was not significantly correlated with the number of its insect herbivores (r_s = -0,80; p>95%) and also not to the number of species of insect herbivores which remained the same throughout the sampling period.

TABLE 13(b) SITE F

Month	July	October	January	April	Analysis
Dry mass of stems / plants (±Std. Error)(g)	46,77 ± 20,93	136,30 ± 27,94	162,93 ± 21,53	214,48 ± 35,77	H = 23,99
No. of insect herbivores/100g dry mass of stems (± Std. Error)	1,47 ± 0,52	0,23 ± 0,09	0,19 ± 0,08	0,35 ± 0,07	H = 2,56
No. of herbivorous insect sp.	4	4	4	4	Chi^2 =0,00

As with Site A, the dry mass of stems of *S. pterophorus* showed a significant seasonal increase at Site F (H = 23,99; p<5%) from July up to April. There was no significant seasonality of the number of insect herbivores (H = 2,56; p>95%) and of the number of herbivorous insect species upon the stems (Chi^2 = 0,00; p>95%). Neither were the correlation coefficients between the dry mass of stems and the number of insect herbivores or number of species of insect herbivores on stems significant (r_s = 0,80; and r_s = 0,50 respectively; p>95%).

With the exception of the generalist *Hilda patruelis* the other more common three species of insect herbivores of *S. pterophorus* stems were borers and are dealt with in more detail in Chapter 6. For this reason no figures are drawn here, but appear in Chapter 6. Although *H. patruelis* was found upon the stems throughout the four seasons it was not possible to estimate its effect upon the dry mass of *S. pterophorus* since it caused no visible damage.

TABLE 14 Seasonality of insect herbivores and dry mass of the stems of *S. inaequidens*.

TABLE 14(a) SITE A

Month	July	October	January	April	Analysis
Dry mass of stems / plants (±Std. Error)(g)	5,57 ± 2,15	5,15 ± 1,47	5,83 ± 1,44	5,94 ± 1,97	H = 2,56
No. of insect herbivores/100g dry mass of stems (± Std. Error)	29,17 ± 6,86	41,23 ± 11,79	43,39 ± 14,72	36,31 ± 11,21	H = -2,39
No. of herbivorous insect sp.	2	4	3	4	Chi^2 =0,85

None of the variables in Table 14(a) were found to have significant seasonal variations (H = 2,56, for the dry mass of stems, H = 2,39 for the number of insect herbivores and Chi^2 = 0,85 for the number of herbivorous insect species).(p>95%).

TABLE 14(b) SITE F

Month	July	October	January	April	Analysis
Dry mass of stems / plants (±Std. Error)(g)	4,71 ± 1,29	5,08 ± 2,12	4,78 ± 1,79	6,15 ± 2,67	H = 6,16
No. of insect herbivores/100g dry mass of stems (± Std. Error)	17,25 ± 6,48	44,91 ± 28,23	22,21 ± 21,42	28,97 ± 32,34	H = 3,71
No. of herbivorous insect sp.	2	4	2	3	Chi^2 =1,00

As with Site A, none of the variables in Table 14(b) above was found to have a significant seasonality (p>95%; H = 6,16 for the dry mass of stems, H = 3,71 for the number of insect herbivores and Chi^2 = 1,00 for the number of herbivorous insect species on stems). Similarly, the herbivory effects of the insects upon *S. inaequidens*' stems could not be easily estimated by way of analysing the dry mass of the host.

5.2.4 SEASONALITY OF INSECT HERBIVORES UPON THE ROOTS

Tables 15 and 16 below show the seasonal data of the dry mass of roots per plant, the number of insect herbivores on roots and the number of herbivorous insect species upon roots of *S. pterophorus* and *S. inaequidens* respectively at Site A and Site F. Only one, and the same, insect species, *H. patruelis* was found on the roots of both plant species in both sites. Although the dry mass of roots could have varied between seasons, it would not be reasonable to relate the number of *H. patruelis* with the dry mass of the roots of the host because the *H. patruelis* is a generalist whose presence or absence depended upon other host plants as well. Besides the dry mass of roots could have been affected by the presence of roots of other plants which were not being sampled and how soft the soil was in order to extract all the root matter. The roots (and stems) were in excessive supply, especially for a generalist, in absence of competition from other herbivores. Factors which kept the population of *H. patruelis* low in spite of the unlimited supply of roots need to be investigated. *H. patruelis* is not known to be serious upon any of its wide range of hosts (ANNEULE AND MORAN, 1982).

TABLE 15 Seasonality of insect herbivores upon the roots of *S. pterophorus.*

TABLE 15(a) SITE A

Month	July	October	January	April	Analysis
Dry mass of roots / plants (±Std. Error)(g)	27,16 ± 5,90	32,82 ± 3,73	25,90 ± 2,16	28,72 ± 3,33	H = 13,13
No. of insect herbivores/100g dry mass of roots (± Std. Error)	14,27 ± 5,28	13,52 ± 0,94	20,75 ± 0,56	27,42 ± 9,39	H = 2,56
No. of herbivorous insect sp.	1	1	1	1	Chi^2 =0,00

The dry mass of roots was significantly seasonal (H = 13,13; p<5%) whilst the number of insect herbivores upon the roots and the number of species of insect herbivores were not (H = 2,56 and Chi^2 = 0,00 respectively; p>95%). However, the highest mass of roots was recorded during October and the lowest during the following sampling session of January. The correlation coefficient between the dry mass and the number of insect herbivores was not significant (r_s = 0,6;p>95%).

TABLE 15(b) SITE F

Month	July	October	January	April	Analysis
Dry mass of roots / plants (±Std. Error)(g)	13,18 ± 5,90	18,22 ± 3,73	16,36 ± 2,16	19,95 ± 3,33	H = 10,77
No. of insect herbivores/100g dry mass of roots (± Std. Error)	27,50 ± 16,63	14,06 ± 4,38	17,96 ± 6,96	13,16 ± 2,92	H = 1,98
No. of herbivorous insect sp.	1	1	1	1	Chi^2 =0,00

The dry mass of roots was significantly seasonal (H = 10,77; p<5%), whilst the number of insect herbivores and the number of herbivorous insect species were not significant (H = 1,98 and Chi^2 = 0,00 respectively; p>95%). A bigger mass of roots was recorded during April, followed by October and the lowest during July. The correlation coefficient between the dry mass of roots and the number of insect herbivores was not significant (r_s = 0,2;p>95%) thus mutual influences could not be elucidated.

TABLE 16 Seasonality of insect herbivores upon the roots of *S. inaequidens.*

TABLE 16(a) SITE A

Month	July	October	January	April	Analysis
Dry mass of roots / plants (±Std. Error)(g)	1,29 ± 0,33	0,89 ± 0,21	1,08 ± 0,21	0,92 ± 0,27	H = 3,40
No. of insect herbivores/100g dry mass of roots (± Std. Error)	147,91 ± 65,84	266,11 ± 108,24	273,10 ± 103,31	286,89 ± 81,73	H = 0,68
No. of herbivorous insect sp.	1	1	1	1	Chi^2 =0,00

The seasonality of the mass of roots, the number of insect herbivores on roots or the number of herbivorous insect species on the roots of *S. inaequidens* in site A as given in Table 16(a) above, was not significant. (H = 3,40, H = 0,68 or Chi^2 = 0,00 respectively; p>95%).

TABLE 16(b) SITE F

Month	July	October	January	April	Analysis
Dry mass of roots / plants (±Std. Error)(g)	1,21 ± 0,62	0,88 ± 0,35	0.85 ± 0,35	0,98 ± 0,42	H = 7,65
No. of insect herbivores/100g dry mass of roots (± Std. Error)	126,09 ± 42,93	174,07 ± 30,77	286,45 ± 91,39	191,37 ± 79,02	H = -18,77
No. of herbivorous insect sp.	1	1	1	1	Chi^2 =0,00

The dry mass of roots was not significantly seasonal (H = 7,65; p>95%), although the number of insect herbivores was significantly seasonal (H = 18,77; p<5%). Highest number of insect herbivores was recorded during January, having increased steadily from July with the lowest number.

Summary of statistical analysis concerning the seasonality of dry mass of parts of the two plant species and their insect herbivores:

- only significant variations are given.

1 Dry mass of plant parts

a) *S. pterophorus*

* There were significant seasonal differences in the dry mass of flowers, foliage, stems and roots at both sites

b) *S. inaequidens*

- There were significant seasonal differences in the dry mass of the flowers and also the foliage at Site F only.

2 Number of insect herbivores / 100g dry mass of plant material

a) *S. pterophorus*

- There were significant seasonal differences in the number of insect herbivores / 100g dry mass of the flowers at Site F and of the foliage at Site A.

b) *S. inaequidens*

- There were significant seasonal differences in the number of insect herbivores / 100g dry mass of flowers, foliage and also of roots at Site F.

5.3 SEASONAL NUMBER OF HERBIVOROUS INSECT SPECIES UPON THE TWO PLANT SPECIES

This section concerns the overall number of herbivorous insect species which were found upon the two plant species over the four seasons. Data has been presented in form of bar - charts to show the nature of seasonal patterns.

Figs 27 and 28 represent the number of herbivorous insect species which were collected during each seasonal sampling occasion for *S. inaequidens* and *S. pterophorus* respectively, combined for the two sites.

Fig. 27 shows that the number of herbivorous insect species increased for the flowers, foliage and overall total from July to January but dropping in April as would be expected. The number of species upon the stems had no discernible pattern while that on the stems remained constant, with only one species, *H. patruelis*. Fig. 29 has a similar pattern to Fig. 27 for flowers, foliage, roots and for the overall total number of species of insect herbivores. The pattern for stems differs between the two figures in that four herbivorous insect species were recruited upon *S. pterophorus* throughout the sampling period. The seasonality of the number of polyphagous insect species could have been greatly influenced by the seasonality of other potential host plant species in the area (listed in Chapter 3, page 20) or by the kind of crops that were cultivated during each season.

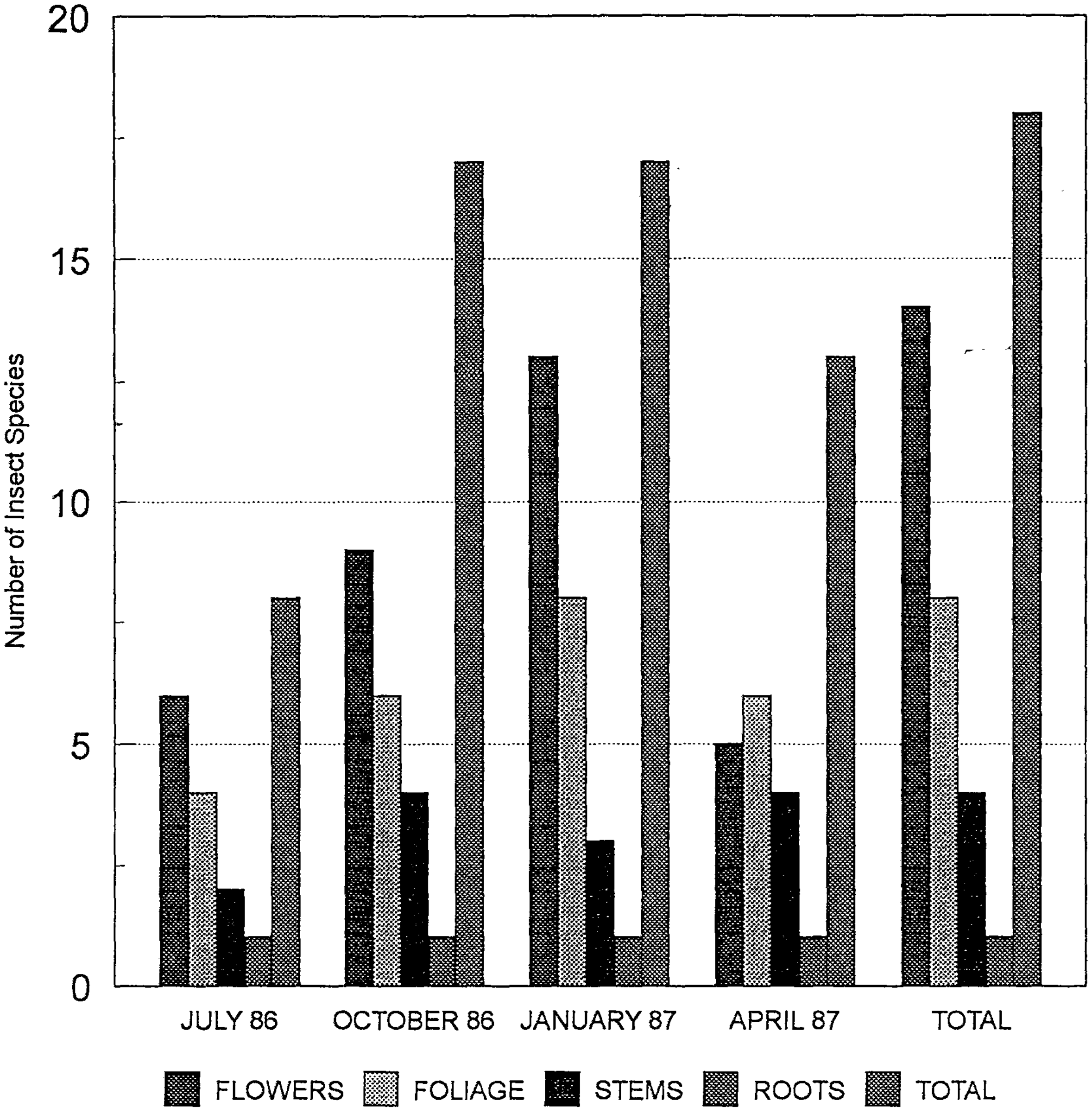


Fig. 27 **Seasonal variations of the number of insect species on *S. inaequidens* during the sampling period**

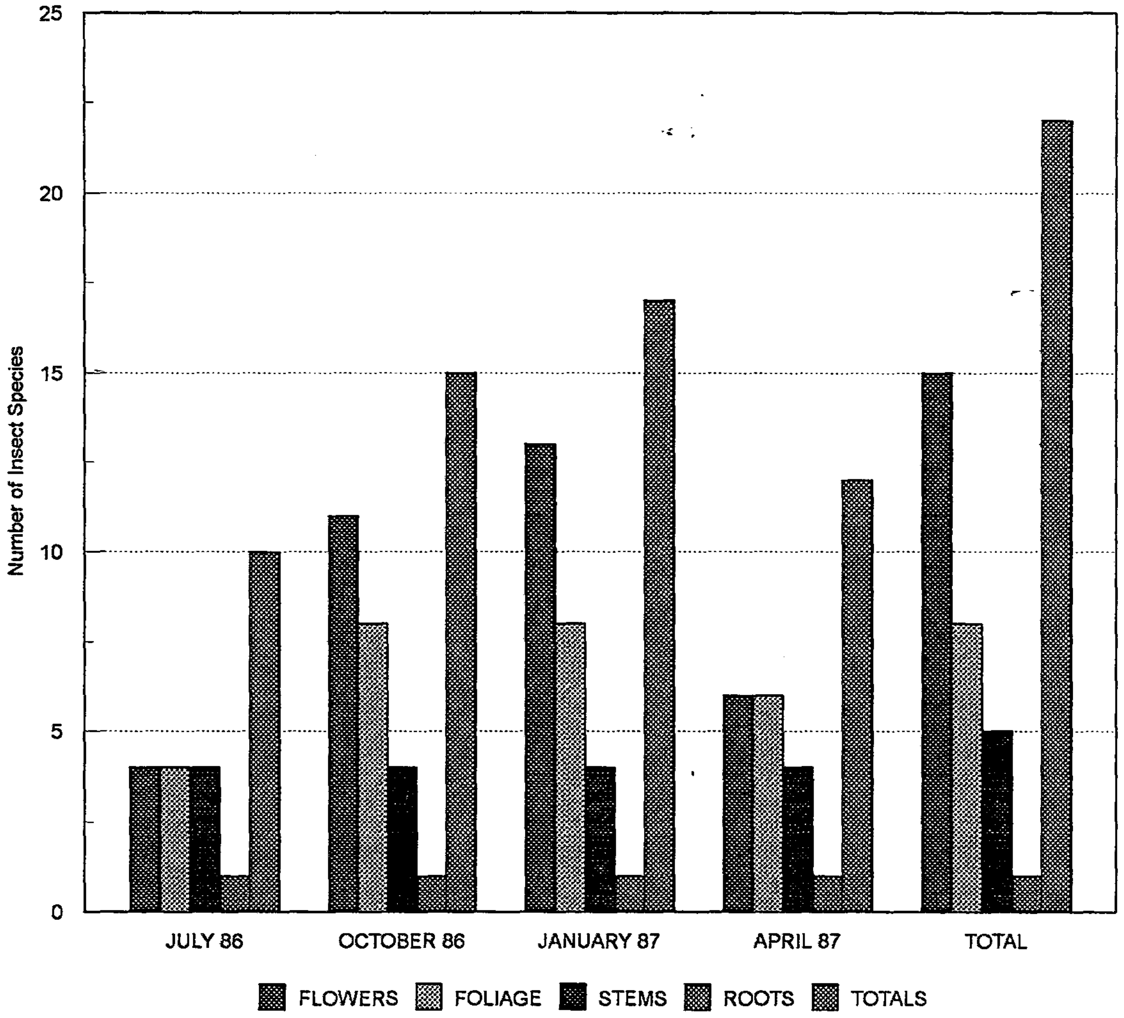


Fig. 28 **Seasonal variations of the number of insect species on *S. pterophorus* during the sampling period**

5.4 DISCUSSION

Results showed that each part of the plant, especially of *S. pterophorus* had a different seasonal growth pattern. Therefore it is necessary to analyse seasonality of each insect herbivore against the part of plant it feeds upon rather than the whole plant.

The dry mass of each part of *S. pterophorus* was increasing throughout the sampling period. Results emphasised the observations in Chapter 2 that *S. pterophorus* was not only biannual but underwent secondary thickening in its stems. *S. inaequidens* was less seasonal and both plant species had overlapping generations in areas where opportunities of disturbed ecosystems were continuous. Results also show that the assemblage of insect herbivores is clearer if samples are taken throughout all the seasons, because some serious insect herbivores, such as *Monolepta* sp. and *Nysius* sp. , may not appear in all the seasons and also because, according to VARLEY, *ET AL* (1973) different conditions may influence the proportion and behaviour of each herbivorous insect species variously. The behaviour, type and proportions of species of insect herbivores were probably affected by seasons since seasons recorded different combinations of insect species.

The correlation between dry mass of most of the parts of plants and the numbers or number of species of insect herbivores which fed upon them was not significant. Some of the more important insect herbivores showed seasonality. Results show no seasonal effects upon numbers of most insect herbivores and most of them were independant of the response of their two host species towards seasons; either the insect herbivores or their two host species would have probably yielded those results in the absence of the other. Therefore the relationship between the populations of insect herbivores and the dry mass of their hosts was obscure. The reason could be that seasonal variations of the dry mass of plants are not a good representative of the availability of such plants to their insect herbivores, or alternatively, the seasonal numbers of insect herbivores, especially generalists are not influenced by the mass of an individual host species because their host range is wide. As a result of the two plant species being opportunists that germinated in any disturbed area during any time of the year, the absence or presence of the two plant species was of no serious consequence towards the generalist insect herbivores. A generalist is perhaps the most likely herbivore for an opportunist. The wide host range of these generalist insect herbivores would mean that they would be affected only minimally by variation in a single opportunistic host species.

Although the species composition of the plant community was not exactly the same in the two sites and probably changed variously seasonally similar herbivorous insect species were collected from the two sites during the four seasons. These results disagree with the suggestion by STRONG *ET AL* (1984) that neighbours influence the recruitment of insect herbivores in that it implies that the kinds of insect herbivores would differ, even if slightly, as a result of the difference in the composition of plant communities in the two sites and also as a result of seasons changing that composition of plant community. That the herbivores were of the same kind may have emphasised the high effectiveness of the defences of the two *Senecio* species compared to other plant species in the sites - i.e. not many other generalists can feed upon them.

While the two sites hosted the same kinds of insect herbivores and predators throughout the four seasons, the number of insects differed at the two sites. Dry mass of the hosts has already been shown not to have affected the numbers of insect herbivores. The difference in numbers of insect herbivores between sites could have been caused by the difference in the structure of vegetation (Chapter 2) and associated micro climatic conditions in each site as suggested by PIMENTEL, D (1961), (REPORTED IN SOUTHWOOD *ET AL*, 1982).

It is possible that by growing in the cold season the two plant species avoid competition with other plants. Another possibility is that by growing throughout the cold season, the two plant species had a relatively insect - free periods. The absence of many of the monophagous or important insect herbivores during winter could have been one of the reasons for their success around Butterworth. Only one important insect species, *Spilostethus,* appeared during the same cold months, probably as a means of its own strategy of securing a competition free feeding period. No stress that could cause death of the whole plant was ever observed during any season. The two plant species were under utilised during all the four seasons such that there was no competition for them, as a result of their opportunistic strategy and chemical protection acquired from alkaloids. Using the scoring system of relative effectiveness of insect herbivores designed by HARRIS (1973), the highest phenological potential, although not adequately serious was shown by *Spilostethus* sp. which is unfortunately a generalist. Therefore there was no insect herbivore that would specifically influence the abundance of *S. pterophorus* or *S. inaequidens* during all the four seasons, and prospects of biologically controlling the two plant species at Butterworth by use of their insect herbivores are quite remote.

Tables showed very high standard errors. This was as a result of the very wide variation in the dry mass of the plants, some of which would have fewer, or no, insects upon them at all.

6. THE STEM BORERS OF *S. pterophorus.*

6.1 INTRODUCTION

Three borer species were recorded in the stems of *S. pterophorus* : *Lixus* sp., *Mordella* sp. and a species of Cerambycidae, the larvae of the latter were not successfully reared and the species was not identified further. The three borer species were considered to be of considerable importance since many of the *S. pterophorus* plants sampled were found to be infested by one or more of these borer species. It was thus decided to carry out a separate and more detailed study of the borer species.

For these studies, a sampling programme was designed, the details of which appear in each of the following sections.

Five flowering plants were picked from each of the two sites, A and F, following the methods described in Chapter 2, every week for 48 weeks, between October 1986 and September 1987. A total of 240 plants from each site (or an overall total of 480 plants) were picked from both sites combined. A further 11 seedlings or young plants were picked to study the nature of immature larvae of *Lixus* and to find out when the plant was first attacked.

In order to identify the most favoured position for the burrows of the three borer species, flowering plants infested either by one of the three borer species or by combinations of them were sampled. The presence of burrows was determined at five centimetre intervals along the stems of plants of 130cm, 150cm, 160cm, 170cm and 180cm height.

Further samples of infested plants were picked to analyse the borer species combinations in plants during March and December.

Observation of the behaviour of adult borers was carried out in the laboratory by use of potted mature plants which were planted in the flower pots at seedling stage and using soil and seedlings from which any insects had been removed and later covered with a muslin gauze cage.

Petri-dishes, transparent drinking straws and stem pieces of *S. pterophorus* of about 10cm length were employed to make more observations about burrowing, irritability or defensive movements of the larvae, especially those of *Lixus*.

The temperature in the laboratory was not controlled but the maximum was found to be on average higher by 4,6 ° C than that outdoors on 12 occasions at noon during October and December. The probable effect of this difference in temperature upon the larvae reared in the laboratory should be kept in mind.

6.2 THE BIOLOGY OF *Lixus* sp. (Curculionidae).

Of the three borer species, *Lixus* sp. was given most attention because adults were more common and were seen feeding upon the foliage of *S. pterophorus*.

6.2.1 STRUCTURE AND BEHAVIOUR OF THE THREE STAGES OF THE LIFE CYCLE OF *Lixus.*

The eggs of *Lixus* sp. were not found. A description of the structure of *Lixus* eggs, and particularly of the eggs of *Lixus cancarus*, Say, the Rhubarb Beetle, is given by KRANZ *ET AL* (1978).

6.2.2 LARVA OF *Lixus* sp.

This was the most frequent stage found and also appeared throughout the sampling period. (Fig. 29; page 93).

The smallest larva was about 1mm. long. By about 5mm of length, the mouth parts were screlotised with orange coloured mandibles. All the larval stages has 12 segments. No moulting was witnessed.

The colour changed from whitish at 1mm length to creamy at maturity, where the mean size was 22 ± 2,33mm long by 6 ± 1,9mm wide. Larvae structure was typical of the genus. (KRANZ, *ET AL*, 1978).

The skin was very flexible but tough - it could for instance not be easily pieced by a pin or *Formica* soldier castes which would once in a while be found dragging the larva of *Lixus*.

The rest of the structures were characteristic of most larvae of borer species and particularly as KRANZ *ET AL* (1978) describes those of *Lixus*.

BEHAVIOUR

The larvae responded vigorously to potential danger, for example, when touched. In a burrow, it would turn to face the offending object and crawl backwards to the far end of that burrow where it would display violent slapping of the substrate by its anterior end, reminiscent of the soldier caste of *Macrotermes*. Similar movements of the posterior end occurred if the disturbance was from that side. The mandibles were kept open and closed on any object coming close enough.

Larvae also responded to vibrations. Tapping the stem section containing a larva would result in audible tapping sounds from the larval thrashing movements.

Larvae could not coexist in a burrow because of this defensive behaviour. This is perhaps the explanation why two or more larvae were never found inside the same burrow in the plants.

Responses to temperature were tested in pith-filled drinking straws and stem sections which larvae had been allowed to enter. They entered without coercion. The end of the straw or stem pieces that were exposed to a warm electric plate or place into ice blocks resulted in the larvae moving away from that end, thus showing that larvae responded to temperature extremes.

The same equipment, as above, was used to make observations about boring activity and the transparency of the drinking straw came in handy. Burrowing could last up to about five hours and one of the factors which determined the duration was the presence of a disturbance. For example, burrowing could be made to continue if there was intermittent disturbance of the posterior end of the larva. Burrowing could also continue as long as one end of the burrow was kept open, since it would immediately set about blocking, by digging out more pith from the other end of the burrow and carry it to block the open end. It would rest a while once the end was closed. It was not clear how the larva sensed the opening or blockade at the ends of its burrow.

Turning in the burrow was accomplished by bending over ventrally or dorsally. The larva was so flexible that it could squeeze itself through narrower openings, such as narrower drinking straws, than the diameter of its body.

Burrowing was achieved by pushing the open mandibles into the plant matter and closing them whilst inserted into the plant material, presumably cutting through the plant material and then pulling the pieces of the plant free. This act was repeated until there was a collection of loose plant material which was then carried toward the other end of the burrow by flexing the head and moving backwards. Larvae did not burrow into fleshy or wet pith, such as that found just behind the shoot and 42 out of the 65 larvae collected during sampling for borer species combinations (Table 18; page 110) were found to be facing towards the shoot of the host. There is no evidence that the collection method could have influenced the larvae to behave that way. Beside, all burrow exits were found in the upper quarter of the burrow thus suggesting that larvae burrowed toward the shoot but without reaching, or eating, through the shoot.

It was difficult to determine the relationship between feeding and burrowing, although just like any other mandibulate larvae, feeding must involve biting into the plant material. The younger larvae could have utilised the pith for their nourishment since their burrows were narrower than the pith diameter, unless they had a way of burrowing across into the vascular system, whilst the older larvae, having consumed all the pith or the pith having disintegrated, as is often the case with mature *S. pterophorus* plants, must have fed upon the vascular system that surrounded them. The intestines of the smaller larvae contained whitish material resembling pith while there were scratch marks upon the vascular system forming the walls of the burrows of older larvae. It was also noticed that mature larvae had burrows whose diameters extended beyond that of the larva's body.

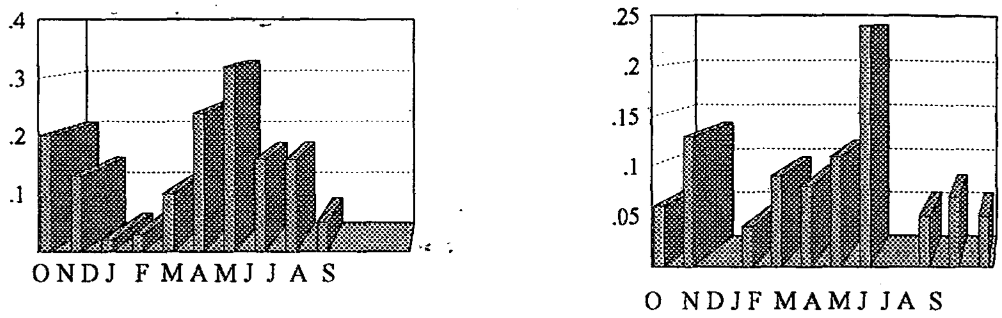
One indication of a mature larva was the presence of a pupation chamber that was as long as the larva but much wider than the rest of the burrow to which an exit window had been constructed which went transversely across the vascular system of the stem but was closed off from the outside by the bark of the stem.

Pupation commenced towards the end of July of the samples which were kept in the laboratory. However, Fig. 29 shows the presence of larvae throughout the 12 months of sampling and pupae were lacking only during December, January and April.

Field observations indicated that the age of the larva corresponded to that of the host such that seedlings contained juvenile larvae while the flowering plants had mature larvae or pupae in them, whatever the time of year. Pupation could not take place outside the burrow and seemed to coincide with the flowering or setting of seed of the host, since no pupae could be found in non-flowering plants.

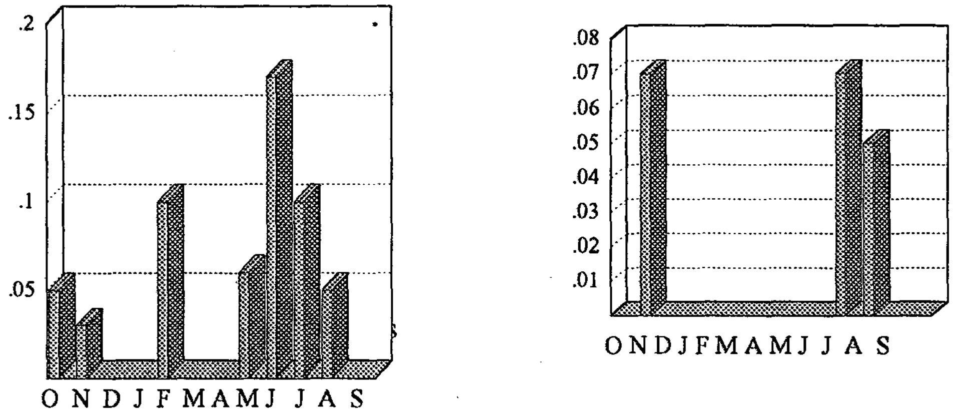
Mortality of larvae was rare within the stems and dead larvae were found only in cases of premature drying of the stem of the host. The other cause of larval death were the parasitoids (Section 6.4).

Larvae in the main stem seemed to be protected even from fires which burnt off the branches and leaves of the host. Such larvae continued to grow and develop and would pupate if the plant regenerated.



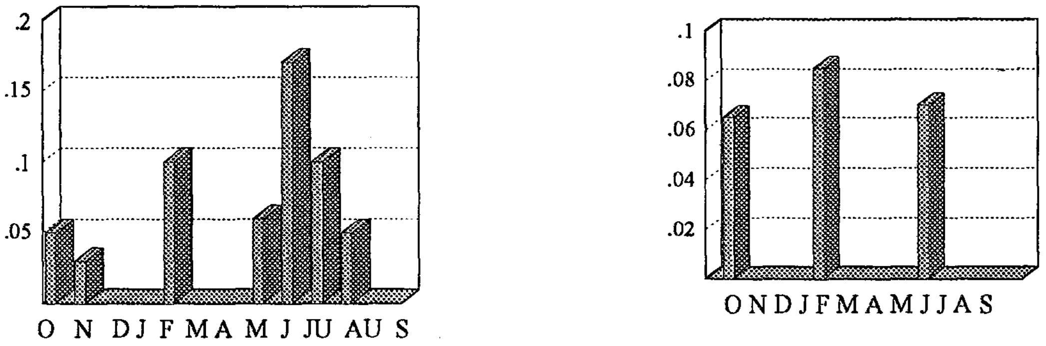
i) Number of larvae/100g dry mass of stems in Site A.

ii) Number of larvae/100g dry mass of stems in Site F.



iii) Number of pupae/100g dry mass of stems in Site A

vi) Number of adults/100g dry mass of leaves in Site F



v) Number of adults/100g dry mass of leaves in Site A

vi) Number of pupae/100g dry mass of stems in Site F

Fig. 29 Seasonal occurence of the three stages of *Lixus* sp.

(Sampling of October 1986 - September 1987)

6.2.2 PUPAE OF *Lixus*

The pupae were, as expected, fewer than the larvae (Fig. 29). Not much can be said about pupae as they are in general a very inactive stage in comparison to the larvae and adults. The size was within the range of that of the mature larva but their colour acquired a touch of amber in some areas of the body on top of the creamy appearance of the larva. It had two sharp ventral hooks on the last segment of its abdomen and two pairs of ventral - lateral rows of hooks along the whole abdomen. Both these kinds of hooks were employed as locomotion organs by digging into the substrate when the abdomen was flexed.

In the laboratory, pupation lasted between six and seventeen days, before the adults emerged. The emergence of the adult from the pupal case was accomplished by active wriggling of the abdomen, which resulted in the pupal cuticle breaking, followed by flexing of the abdomen such that the whole body moved forward. The substrate needed to be rough and moist for the cuticle to break free easily. This was shown by the observation that pupae in petri-dishes or in very dry stem pieces had difficulty; or totally failed; to shed their cuticles.

6.2.3 ADULTS OF *Lixus*

Despite the fact that adults were seen throughout the sampling session of 12 months in the field, very few appeared on the collected plants (Fig. 29). Many could have escaped during the sampling exercise, unlike the larvae or pupae, such that their numbers could have been higher than depicted by Fig. 29. They could also have been feeding upon other plant species.

STRUCTURE

The general shape was that of common members of Curculionidae, with a snout often as long as about half the whole length of the body, but with variable length.

The newly emerged adult was of a dark creamy colour, but dark patches of brown started to appear by the second day. At the end of about four days the whole body was of a dark brown colour. After about a month, the elytra showed golden yellow or cream mixed with dark brownish hair-like structures which were embedded in pits which were arranged in rows along the elytra. This mixture of colours gave the mature adult a mottled appearance of various patterns - there was no specific pattern of colour patches. The mottled appearance camouflaged the adult well in the normal environment. The elytra picked up pollen when rolled over the flower and acquired the colour of pollen. There is thus the possibility that the hair-like structures on the elytra pick up loose matter from the immediate environment so that the insect becomes camouflaged against its immediate environment.

The size of the adult ranged from 15mm to 23mm long (mean ± Standard Error); (mean = 19,13mm ± 0,5) and from 4mm to 5mm wide (mean = 4,7 ± 0,2); (52 individuals of mixed sex). The sexes were identified from seeing them mating. The males length ranged between 17,00mm to 21,00mm (mean = 18,67mm) and the width ranged between 4,00mm to 5,00mm (mean 4,30mm) - 3 males measured. The five females identified measured 20,2 ± 0,71mm long and 4,60 ± 0,22mm wide. This would imply that the males were smaller than the females.

Although the adults were well equipped with wings, none was ever seen flying. They used to walk slowly. No adult was found feeding in the field, but in the laboratory when offered potted plants of *S. pterophorus* and *S. inaequidens*, *Lixus* adults preferred *S. pterophorus*. The adult sat on the leaf margin and ate along the margin with a trimming effect, like one using a pair of scissors, such that the trimmed piece of leaf disappeared into its mouth with the aid of palps. Many Lepidoptera larvae feed the same way.

That kind of feeding left a disfigured leaf which in many cases was not totally eaten. There seemed to be no choice of leaf in terms of size, position or age. Feeding in the laboratory was rare, but lengthy.

BEHAVIOUR

Adults stayed within the plant canopy most of the time, especially during the day, but occasionally walked down the stem to burrow into the soil in which they could spend some time before coming up again.

MATING

Mating was preceded by courtship as follows:

The male walked to the female and after staying obliquely by the female's side moved its head closer with its antennae tapping the head of the female. The male then proceeded to mount upon the dorsal side of the female, approaching from a lateral posterior end of the female. The male could be rejected at this stage, but if not, copulation proceeded. Rejections were frequent and copulations lasted from about 15 minutes to as long as 4 hours and all took place upon the plant. Mating couples could move about on the plant.

LAYING OF EGGS

No female was seen laying eggs, but KRANZ *ET AL*, (1978) gave the methods used by some *Lixus* females, that adults scrape pockets into the host , into which they lay eggs.

The size of plant upon which eggs were laid or into which larvae entered was investigated by studying a sample of infested seedlings and young plants of *S. pterophorus.* Infested plants at an early stage of their growth had a dark mark on the outside of the stem which seemed to lead to the lower end of the burrow of the larva inside the stem. This mark often ran across the vascular system towards the pith and was corresponding with the lower part or end of the burrow and was assumed to be the original entrance into the pith. Only the plants in which the dark mark corresponded with the bottom end of the burrow were used to obtain the results in Table 17 below.

TABLE 17 Position of burrow entrance on seedlings of *S. pterophorus.*

Height of plant/cm	Distance from the ground to the burrow entrance/cm	Distance from plant shoot to the burrow entrance/cm	Length of larva/mm
10,5	10,0	0,5	1,0
18,0	15,5	2,5	2,0
25,0	23,8	1,2	dead
27,0	22,5	4,5	dead
28,5	24,5	4,0	5,0
30,0	27,0	3,0	dead
31,0	24,5	6,5	7,0
33,0	24,5	8,5	8,0
34,0	32,5	1,5	2,0
42,0	36,0	6,0	5,0
43,0	39,0	4,0	4,0

Spearman's rank correlation coefficient showed no relationship between the height of the plant and the dark mark or "shoot to burrow entrance" and also between the length of the larva and the height of the plant (r_s = 0,40 and r_s = 0,35 respectively; p>95%). There was however, a significant and positive correlation between "shoot and burrow entrance" and the length of larvae (dead larvae excluded) with r_s = 0,98; (p<5%).

That there was no significant association between the size of the plant and "shoot to burrow entrance" and also between size of larvae and size of the plant seemed to imply that eggs were being laid or larvae entered the plants of various heights or age, but with the young stems, since young larvae were never found in matured stems. The significant correlation between the length of larva and the "shoot to burrow entrance" implied that the eggs were laid or larvae entered through the shoot of the plant, which in any case would be the softest part of the stem, such that the distance between the ground and the burrow entrance could be an indication of the height when the eggs were laid or when the larvae entered, especially since the larvae were probably burrowing upwards.

Some young branches of matured plants contained young larvae. Therefore, eggs were laid upon or larvae entered plants which were soft - softness or penetrability of the stem seems to have been a criterion of choice.

6.3 EFFECTS OF *Lixus* UPON *S. pterophorus.*

There was no sign of mass loss, change in shape or reduction in productivity of *S. pterophorus* caused by *Lixus* sp.. The only serious defect was the death of the plant shoot in cases where the larva chewed its way close to the shoot, or when the larva had matured. However, some infested plants with mature larvae did not have dead shoots. In a few cases, the presence of the *Lixus* sp. larva close to the shoot caused a gall formation. (i.e. a dead shoot or a gall would be signals of the presence of the larvae of *Lixus* sp. although not all infested plants had these signals). The presence of a dead shoot or a gall seemed to induce extra branching at lower positions of the stem.

6.4 THE PARASITOIDS OF *Lixus.* sp.

Two closely related hymenopterous parasitoids attack the larva of *Lixus* sp., both belonging to Superfamily Ichneumonoidea and Family Ichneumonidea. These are still to be identified further. They had extraordinary long ovipositors and some had a golden colour while others were blackish with golden patches.

There were no structural or behavioural differences between parasitised and unparasitised larva of *Lixus* sp.. The parasitised larvae formed a special oval-shaped brownish cocoon cases inside which was one glabrous whitish larvae of the parasitoid. Unparasitised *Lixus* sp. larvae never formed cocoons. Pupation took place inside the stems and adults emerged about two weeks later than the adults of *Lixus* sp., developing from the same generation of uninfected larvae. None of the parastoids appeared in the seasonal collections of insects. However, many were seen flying among the branches of flowering plants of *S. pterophorus.*

6.5 NATURE AND POSITION OF BURROWS IN THE STEMS OF *S. pterophorus.*

This section deals with burrows of all the three borer species of *S. pterophorus.*

The nature of the burrows of each borer species was studied.

NATURE OF BURROWS

Lixus sp. burrows were smooth and without excreta. They were relatively straight and well sealed that the burrows' ends were distinct, especially towards maturity. At the maturity of the larva, the burrows of *Lixus* were much wider than the pith, and had an even wider chamber, with an exit window, in which larvae pupated and adults emerged. This chamber was usually in the upper quarter of the burrow. *Lixus* larvae which matured in stems of non-flowering plants formed bulb - shaped galls perhaps as a result of the larva having to construct a pupation chamber in a narrow stem.

The burrows of the Cerambycidae larva were narrower than those of *Lixus* and the pith, and zigzagged in the pith. These burrows had black solid bodies all along their length but had no exit window, probably because none of these larvae reached maturity.

Mordella burrows were the narrowest of the three and were, like those of *Lixus*, without any matter other than the pith powder. *Mordella* also drilled an exit hole which ran almost horizontally through the vascular system of the stem toward the bark of that stem.

In order to determine the positions of burrows, a special sampling session was carried out during the later half of December and then the first half of March. Infested flowering plants were picked and grouped according to height. Each stem was opened and the burrows of each borer species identified. The presence, or absence, of a burrow was noted at 5cm intervals up the stem. Figs. 30 to 36 show the number of times burrows of each of the borer species appeared at intervals of 5cm along the stem, out of each group of plants.

Positions of burrows are represented by Figs. 30 to 36. The vertical axis represents the height of the plant from the ground and the horizontal axis represent the number of plants with a burrow at a particular height.

Figs. 30 to 33 represent the number of burrows of *Lixus* in plants of 130cm, 150cm, 160cm and 180cm height respectively. From those figures it appears that *Lixus* sp. burrows never reached the shoot of the plant, and were more frequent from 20cm of height of the stem or length of branch whatever the overall heights of the plants were. This height is close to the average of "ground to burrow entrance" realised in Table 17. Figs. 30, 31, 32, 33 and 36 show that the presence, or absence, of other borer species did not change the pattern of positions of burrows of *Lixus* sp.

The burrows of the species of Cerambycidae were more frequent between the base and 50cm of height of the stem (Figs. 35 and 36). For no explanation as yet these burrows seldom appeared in the branches. Probably, this species of Cerambycidae entered the hosts before branching. Figs. 33 and 36 shows that the presence of other borer species did not change the positions of Cerambycidae.

Figs. 34 and 36 shows the burrow distribution of *Mordella.* It shows that this insect species was more frequent between 40cm and 140cm of height of the stem. Fig. 34 shows that *Mordella* was also not affected by the presence or absence of other borer species since its pattern is similar to that of Fig. 36.

No two or more borer species, or individuals of *Lixus* sp. shared a burrow but there were indications of *Lixus* sp. burrowing through the burrows of either

Mordella sp. or species of Cerambycidae as a result of *Lixus* sp. making wider burrows.

Fig. 36 show that the positions of the burrows of the three borer species overlapped in plants of the same height (180cm) which were infested by the three borer species at the same time. *Mordella* sp. could be found above or at the same positions, never below, the burrow or larva of *Lixus* sp. while the species of Cerambycidae could be above and below the *Lixus* sp. burrows or larva, and was often closer to the base of the stem than *Lixus* sp. and *Mordella* sp. A single plant could contain the three borer species in various combinations at the same time.

Open burrows that had been vacated by the species of *Cerambycidae* and *Lixus* sp. hosted various other insect species. In certain cases adventitious roots developed from the stem and grew into its own vacated burrows.

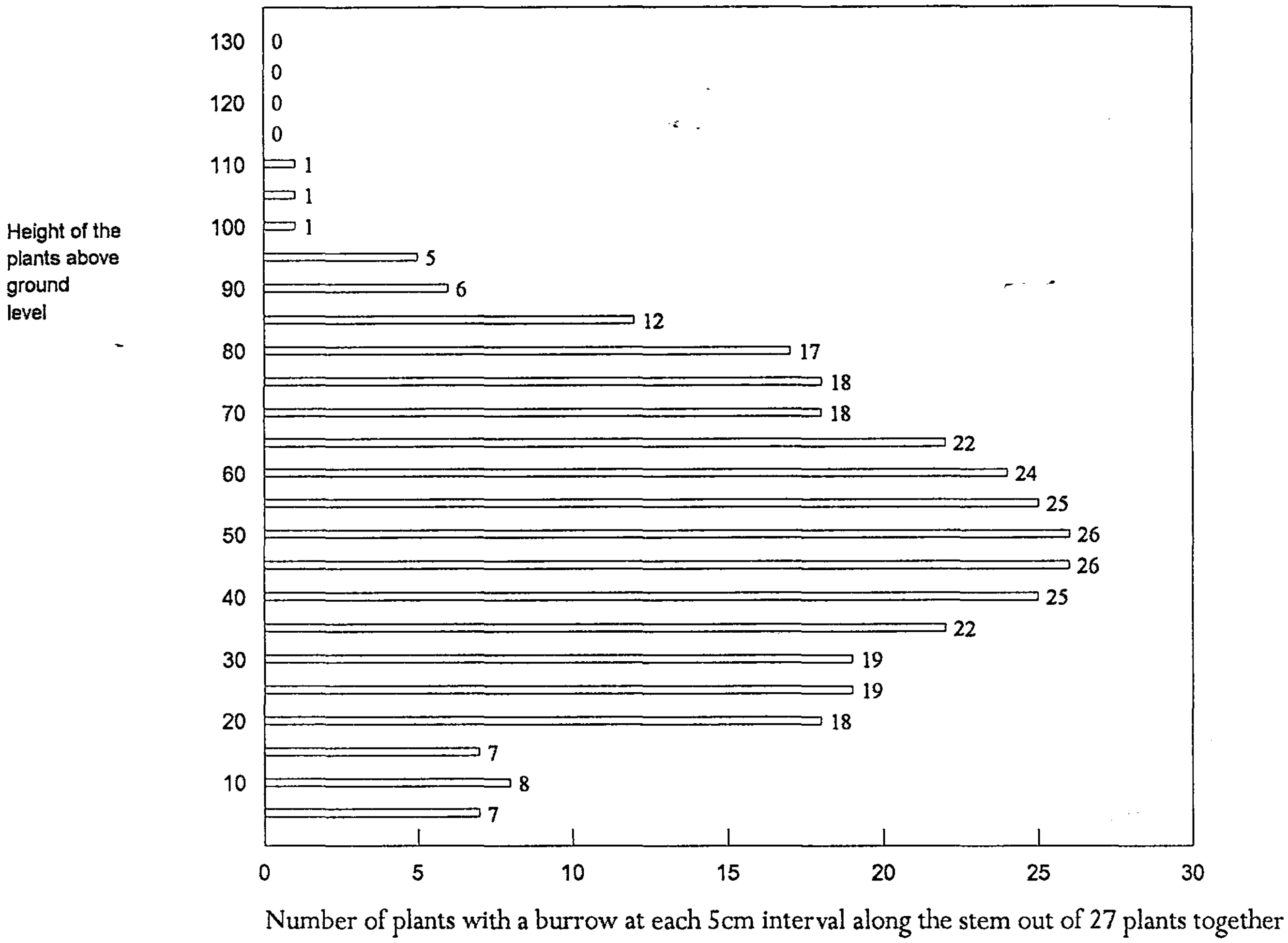


Fig. 30 **Number of plants out of 27 plants of height of 130cm with a burrow of *Lixus* sp. at different positions along the stem. Some of these plants had other borer species.**

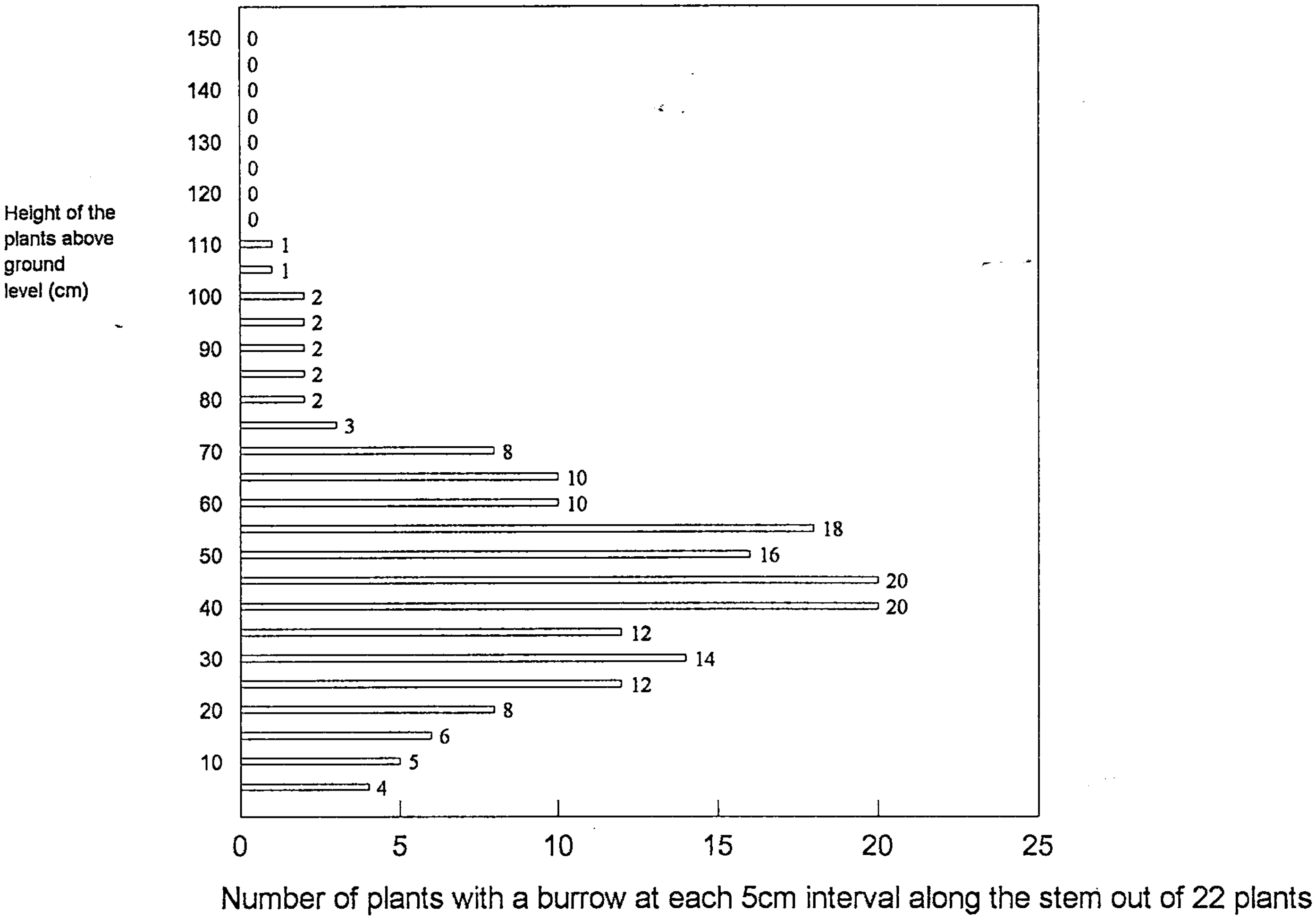


Fig. 31 **Number of plants out of 22 plants of height of 150cm with a burrow of *Lixus* sp. at different positions along the stem. Some of these plants had other borer species.**

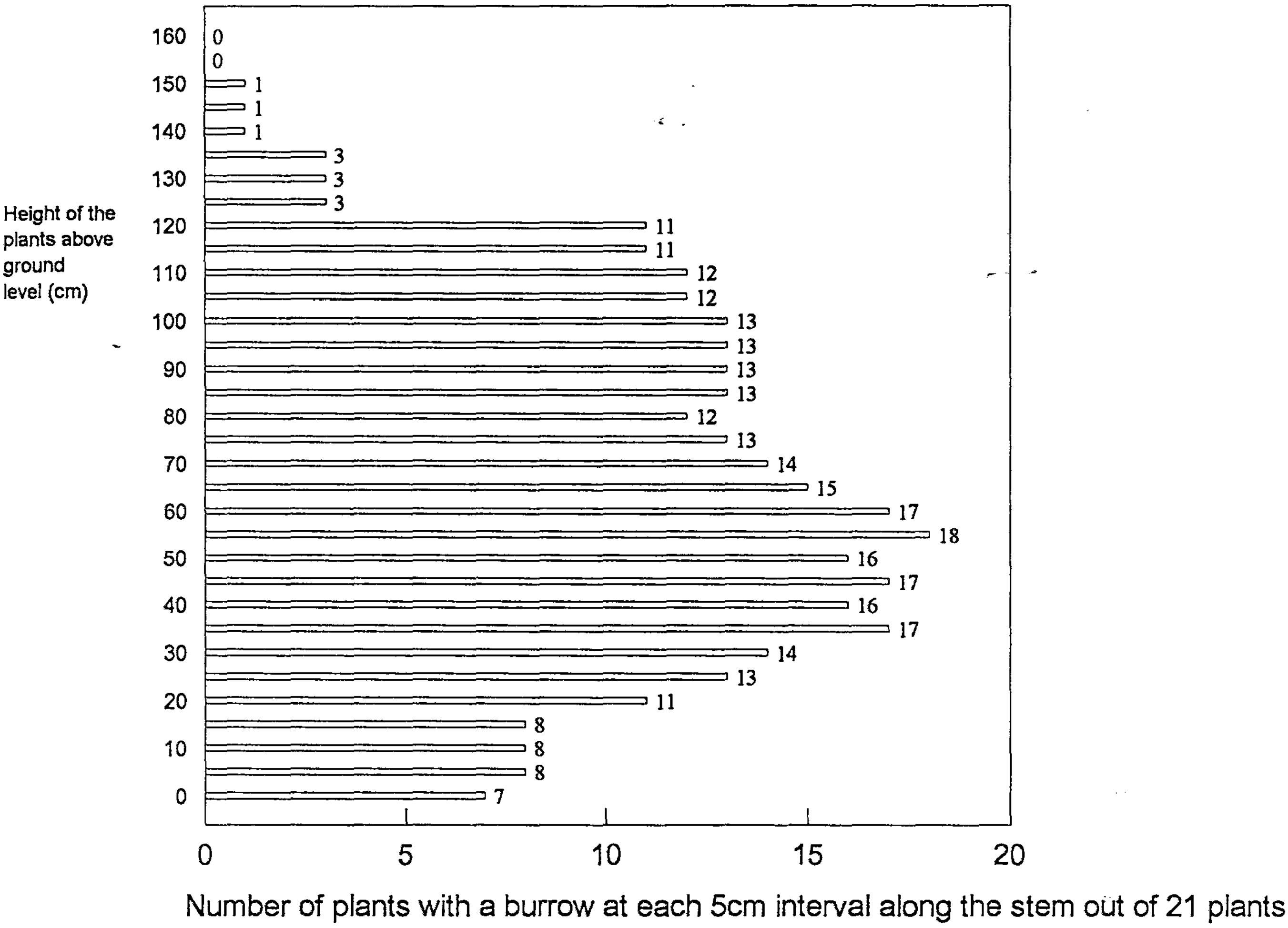


Fig. 32 **Number of plants out of 21 plants of height of 160cm with a burrow of *Lixus* sp. at different positions along the stem. Some of these plants had other borer species.**

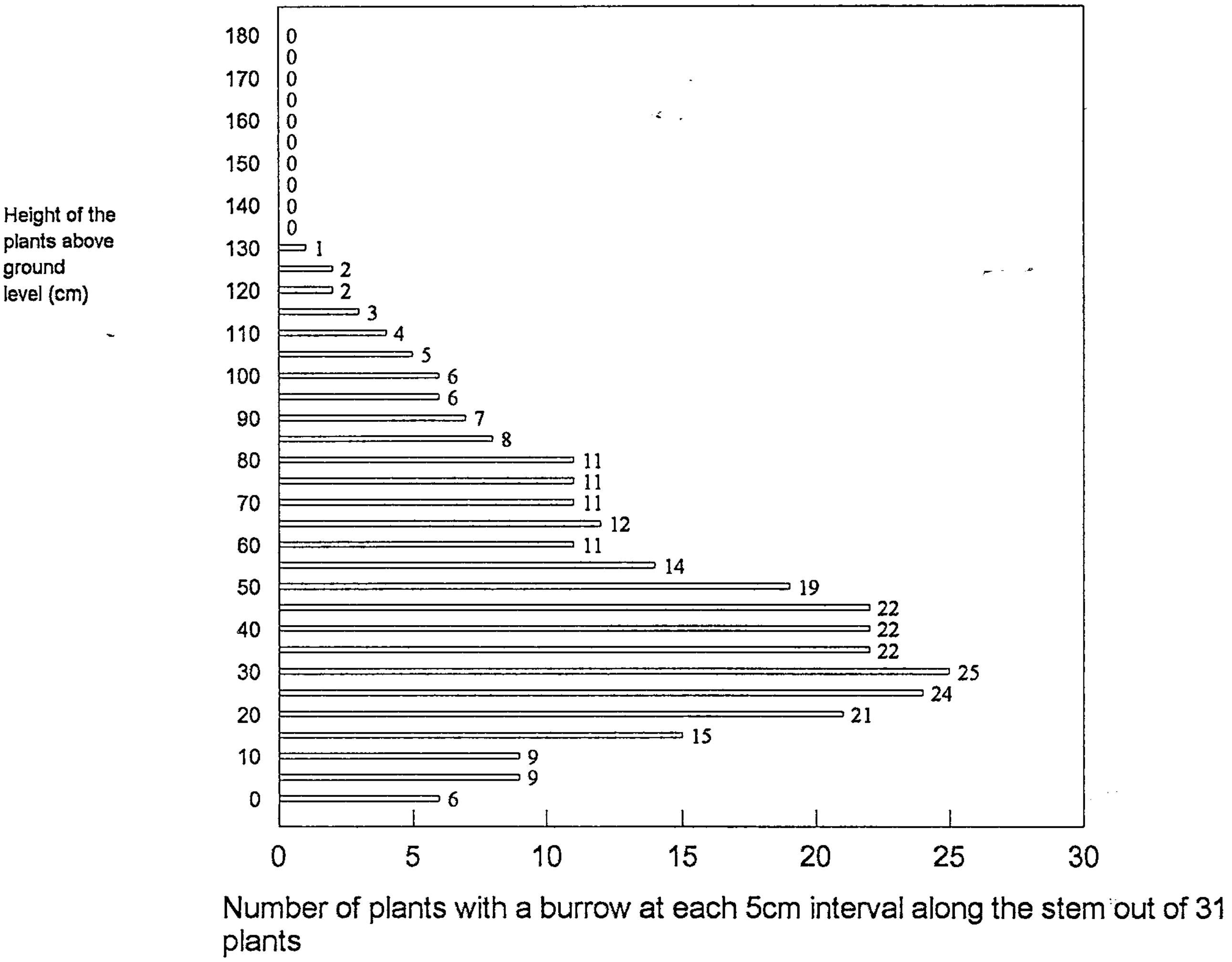


Fig. 33 **Number of plants out of 31 plants of height of 180cm with a burrow of *Lixus* sp. at different positions along the stem. No other borer species were present.**

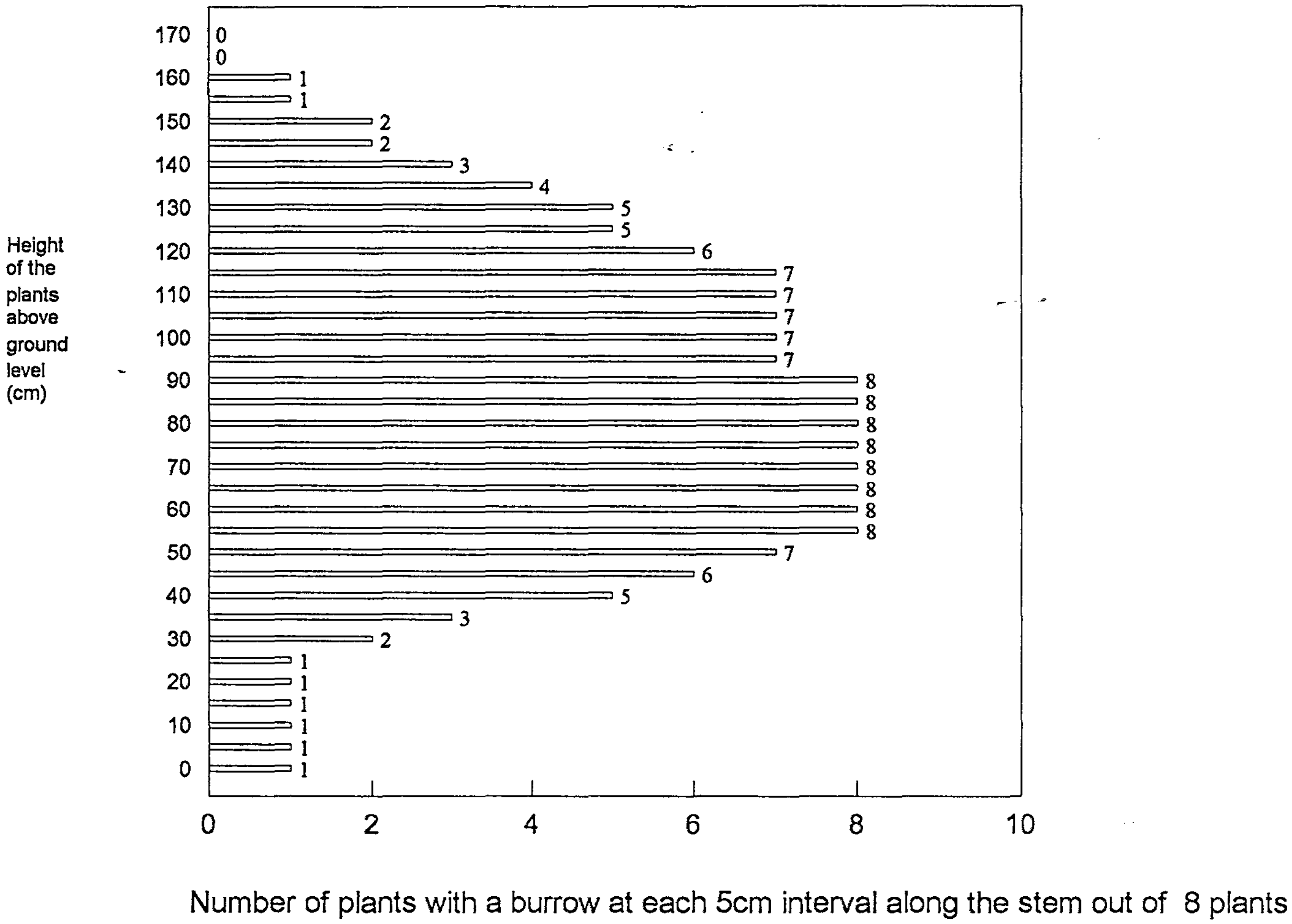
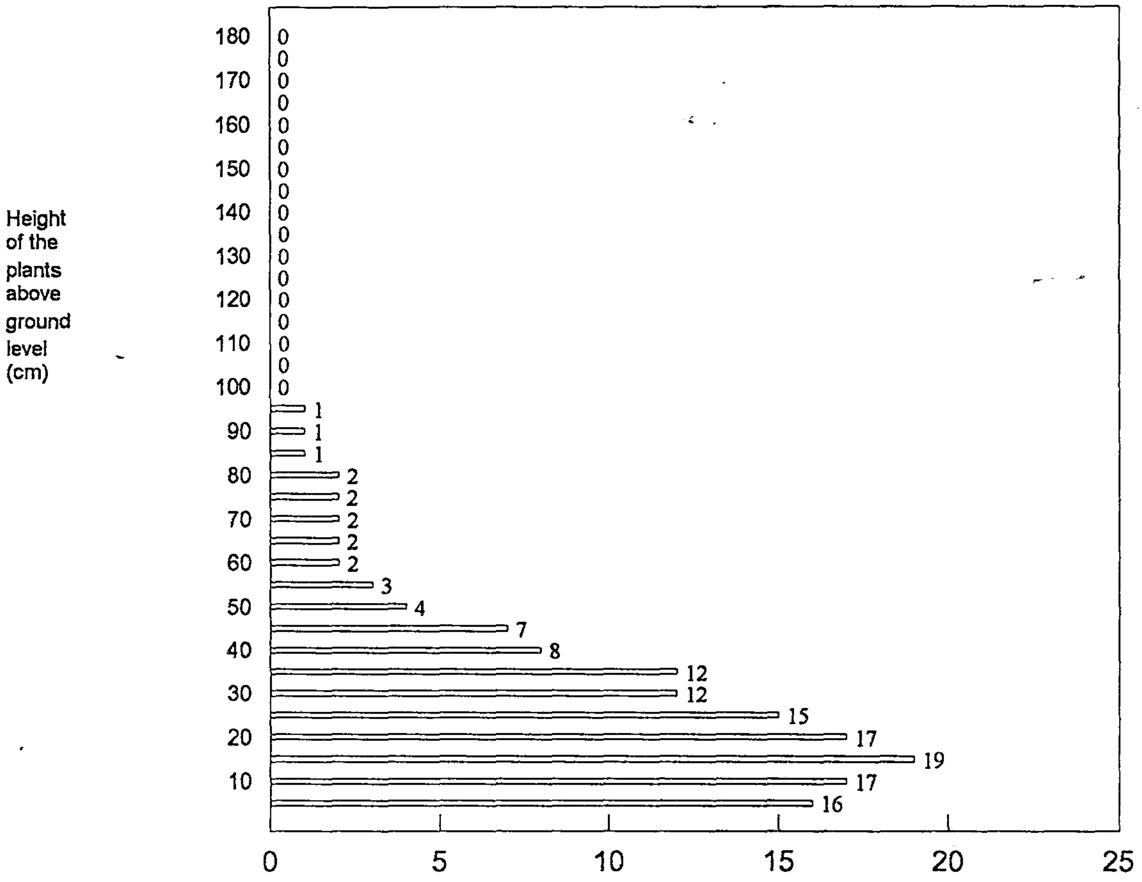
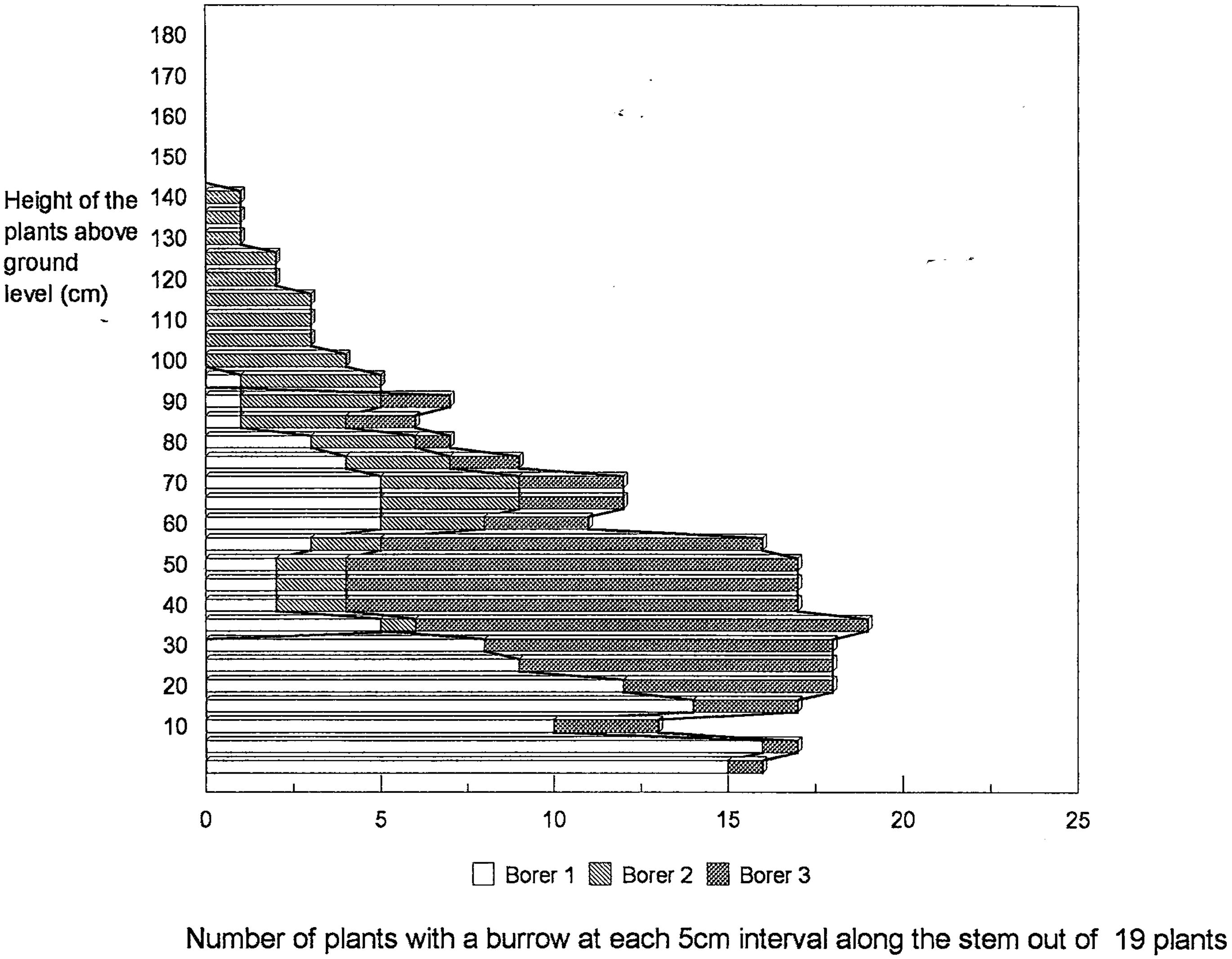


Fig. 34 **Number of plants out of 8 plants of height of 170cm with a burrow of *Mordella* sp. at different positions along the stem. Some of these plants had other borer species.**



Number of plants with a burrow at each 5cm interval along the stem out of 19 plants

Fig. 35 Number of plants out of 19 plants of 180cm height with a burrow of a species of Cerambycidae at different positions along the stem.



Borer 1 - A species of Cerambycidae
Borer 2 - A species of *Mordella* sp.
Borer 3 - A species of *Lixus* sp.

Fig. 36 **Number of plants out of 18 plants of height of 180cm with burrows of all three borer species along the stem.**

6.6 FREQUENCIES OF THE BORER SPECIES IN *S. pterophorus*.

The results presented in this section can be used to compare the incidence of the three borer species as an estimate of the success of each borer species. The three borer species were collected from the same plants, so the total mass of the plants were the same. There was no evidence of host selection according to size or mass and the maximum capacity for a given number of borers or borer species could not be ascertained. This section therefore gives the numbers (in Table 18) of each of the larvae of the borer species found in, and the number of infested plants, of the 480 plants that were sampled from Site A and Site F. The percentages that are calculated represent the number of borer infested plants out of the 480 plants that were sampled. These percentages indicate the probability of finding a plant infested with a particular borer species or combination of borer species. It should however be borne in mind that the population or frequency of each borer species may have been regulated by other factors besides availability of *S. pterophorus* such as its defences against herbivory. A very small proportion was infested (Table 18). Individual plants which were infested by either of the three borer species were not consumed completely and showed no stress as a result of being infested by the borer species. Of the other factors which could have controlled the population of *Lixus* sp.. were its parasitoids (see Section 6.4, page 113).

TABLE 18 The numbers and percentages (in brackets) of plants that were infested by the three species of borers alone or in combination with others. Larvae only were considered in this table.

Plants with *Lixus* sp. only		**41**	**(8,5%)**
Single larva / plant		36	(7,5%)
2 larvae / plant		2	(0,4%)
3 larvae / plant		3	(0,6%)
Plants with the species of Cerambycidae only		**59**	**(12,3%)**
1 Larva / plant		49	(10,2%)
2 larvae / plant		9	(1,9%)
3 larvae / plant		1	(0,2%)
Plants with *Mordella* sp. only		**21**	**(4,4%)**
1 Larva / plant		19	(4,0%)
2 larvae / plant		2	(0,4%)
Plants with *Lixus* sp. and the species of Cerambycidae		**8**	**(1,7%)**
2 *Lixus* sp. + 1 of the species of Cerambycidae		3	(0,6%)
1 *Lixus* sp. + 1 of the species of Cerambycidae		4	(0,8%)
1 *Lixus* sp. + 2 of the species of Cerambycidae		1	(0,02%)
Plants with *Lixus* sp. and *Mordella* sp.		**4**	**(0,8%)**
All of them had 1 *Lixus* sp. and 1 *Mordella* sp.			
Plants with *Mordella* sp. with species of Cerambycidae		**1**	**(0,2%)**
This plant had 2 *Mordella* sp. larvae and 1 larva of the species of Cerambycidae.			
Plants with the three borer species together		**4**	**(0,8%)**
(1 larva of each borer species).			
Plants with each of the borer species in whatever combination:			
Lixus sp.	65 larvae		
(1.14 larvae / plant)		57	(11,9%)
Species of Cerambycidae	84 larvae		
(1.17 larvae / plant)		72	(15,0%)
Mordella sp.	33 larvae		
(1.10 larvae / plant)		30	(6,3%)

Table 18, above, shows that most plants would be found with Cerambycidae (15%), followed by *Lixus* sp. (11,9%) and lastly by *Mordella* sp. (6,3%). From tables above the number of larvae of Cerambycidae was 84, for *Lixus* sp. 65, and for *Mordella,* 33. (From the 480 plants). The average number of larvae per host was not so different for each borer species - it was calculated as 1.16 larvae of Cerambycidae per plant, 1.14 larvae of *Lixus* sp. per plant and 1.10 larvae of *Mordella* sp. per plant. These figures show that each individual host accepts approximately 1 larva of each species. Results show that most infestations were singles, contrary to the indication that, *Lixus* species for example, lay many eggs in one pocket (KRANZ *ET AL*, 1978). There were very few triple occurrences of larvae while the occurrence of the three borer species in one plant was also scarce. It is also interesting to note that *Lixus* sp. and Cerambycidae coexisted more often than any other combination of different borer species although they were found to be utilising the same position of the stem. There was no indication that the various combinations of borer species were influenced by season. Factors which prevented more eggs or larvae, or which determined the number of borers, or the number of borer species, to develop in an individual host need to be investigated, but it seems the presence or absence of another borer species was not affecting the population density per plant of another and that was also the case with the positions of their burrows.

The frequency of each borer species was positively correlated with the population density per plant in that the highest density per plant (1.17) was recorded for the species of Cerambycidae which was most frequent (15%) while the lowest was for *Mordella* sp. with a frequency of 6.3% and a density of 1.10 larvae per plant.

There were also very few triple larvae of the same species (*Lixus* sp.; 0,6% and the species of Cerambycidae; 0,2%) and no such triples were found combined with any of the other borer species. The species of Cerambycidae existed in triples less often than any other borer species although it was the most frequent. It is probable that this species of Cerambycidae layed the least number of eggs upon each individual plant host.

6.7 CHARACTERISTICS OF *Mordella* sp. AND THE SPECIES OF Cerambycidae.

The larvae of these two species were smaller than *Lixus* sp.. Both had those features characteristic of Coleopteran borer larvae. Larvae of all the three borer species were absent in thick stems. Cerambycidae larvae never pupated in the stem of the host; no pupa was found in the field nor did any of the larva pupate in stem pieces in the Laboratory, as was the case with *Lixus* sp. *Mordella* sp. larvae pupated in the stem after creating a chamber which lay transversely across the vascular system, in the stem.

Figs. 37 and 38 below show the seasonal distribution of the larvae and pupae of Cerambycidae; as well as those of *Mordella* sp. along with the adults of

Mordella sp. The species of Cerambycidae constituted the highest number of larvae of the three borer species and, like *Lixus* sp., appeared throughout the sampling period. *Mordella* species had the highest number of adults of the three borer species and all of *Mordella* sp. stages were seasonal, appearing mainly during October up to February and then around August and September.

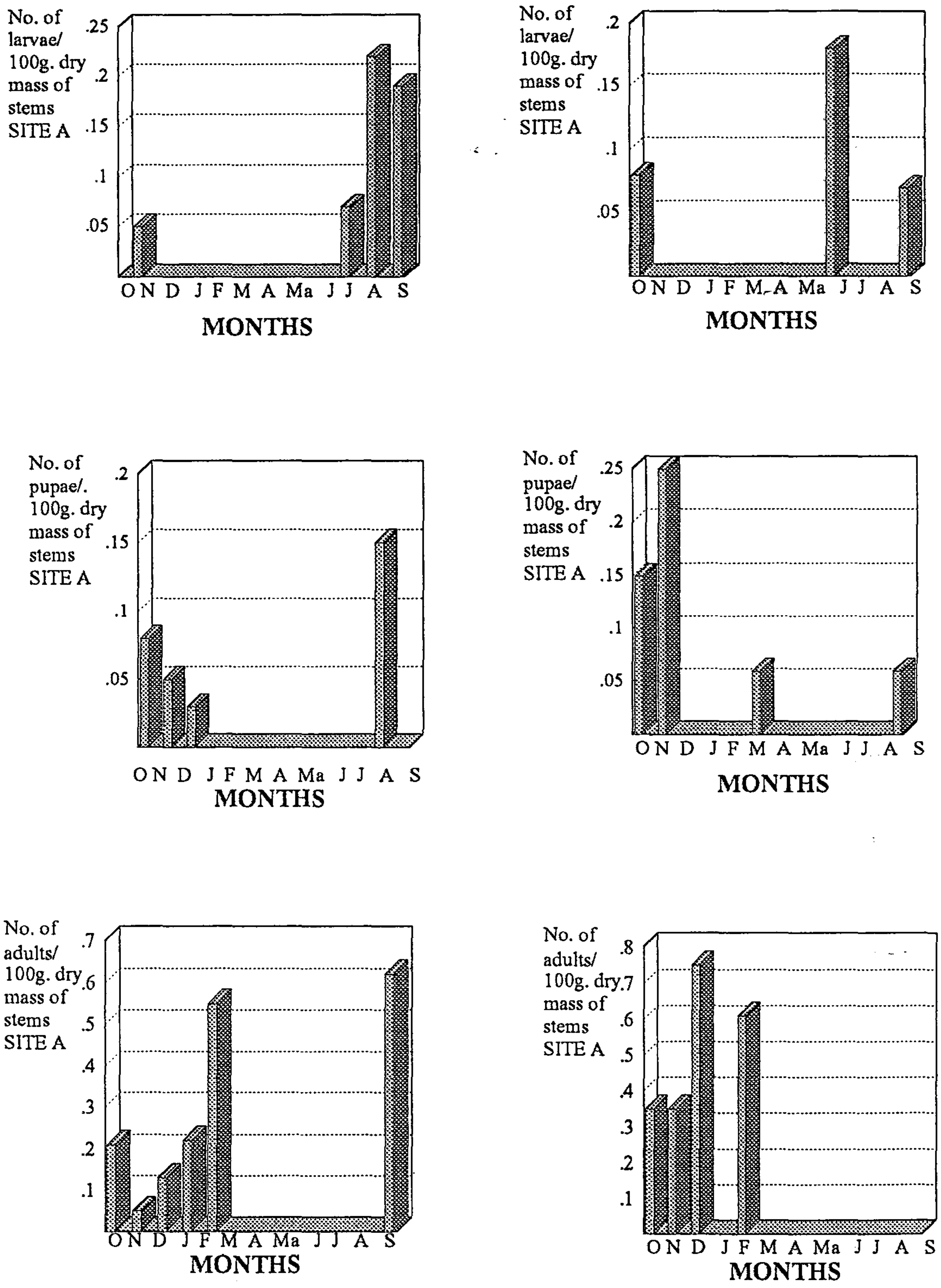
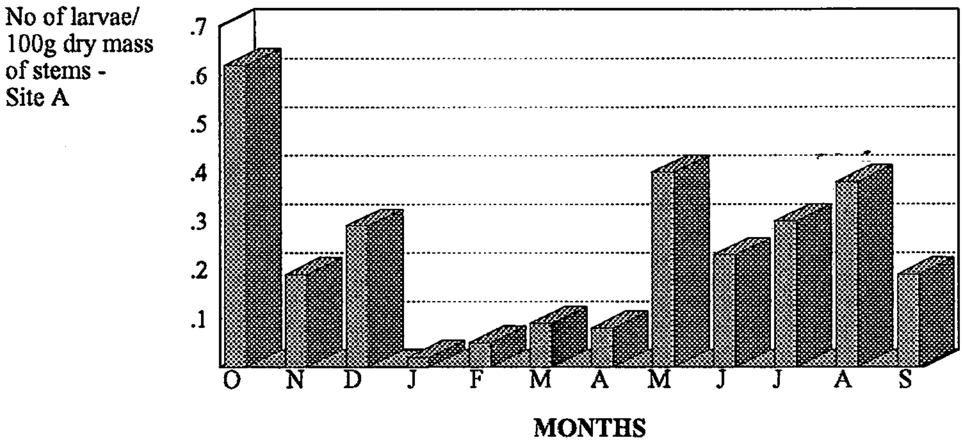
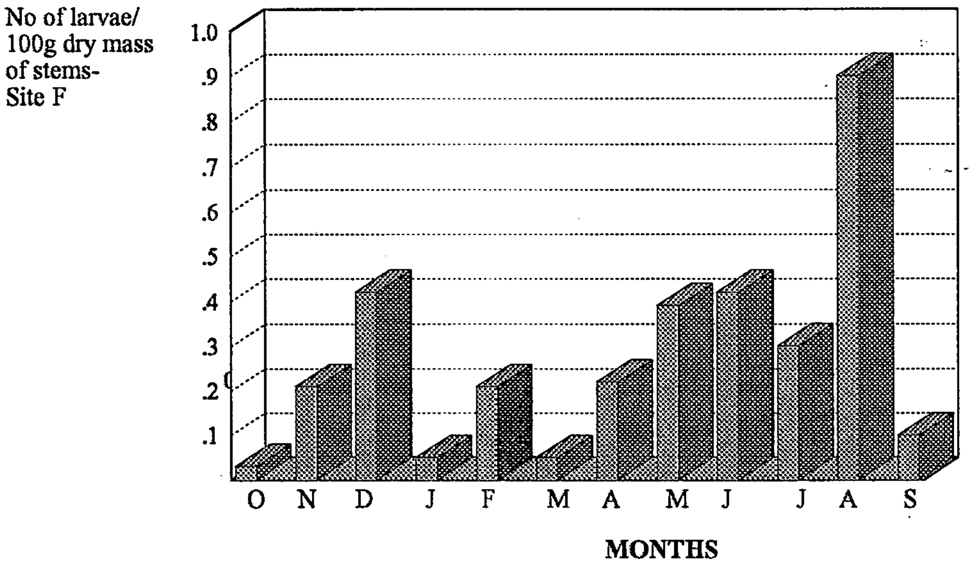


Fig. 37. **Seasonal occurrence of the three stages of *Mordella* sp. (Sampling between October 1986 - September 1987)**



i) Number of larvae / 100g dry mass of Stems in Site A.



ii) Number of larvae/100g dry mass of stems in Site F.

Fig. 38. **Seasonal occurence of a species of Cerambycidae larvae in the two sites, A and F. (Sampling from October 1986 - September 1987)**

Larvae of *Mordella* sp. move along by forming loops. The pupae of *Mordella* sp. were similar to those of *Lixus* sp. but much smaller. Their colour ranged from pale cream to amber as they developed to form adults.

In its behaviour, the larva of *Mordella* sp. was not as sensitive or aggressive as that of *Lixus* sp. but seemed to seek crevices or covered places. It seemed to be able to burrow into the stem vascular system at a faster rate than that of *Lixus* sp. Its burrowing resulted into very fine pieces of pith or wood. Unlike the larvae of *Lixus* sp. the *Mordella* sp. larva could attach itself firmly, by its pro legs, onto any kind of solid surface and could burrow into a wide variety of Compositae stem pieces it was put upon in the Laboratory, and even developed to pupate although no adult *Mordella* sp. ever emerged from these other compositae stem pieces in the laboratory or seen on these other plant species in the field.

The pupae behaved in a similar manner to that of *Lixus* sp. while the adult was a very restless, hopping and flying phytophage. The adult was never seen feeding although it was found in the foliage. Mating commenced soon after emergence of the adult and took place on the host. It was not seen where it laid eggs.

6.8 DISCUSSION

It looks like the largest borer species, *Lixus* sp. was the more important borer in the lower part of the stem in comparison with the smaller

Cerambycidae in terms of the volume or length of stem it's burrows occupied, but larvae of the species of Cerambycidae were most numerous. *Mordella* sp. was more often than not occupying the upper part of the stem and its positions coincided with the region with most branches, within the canopy. There was probably no significant competition especially since the three borer species could occupy the same plant and adjacent or overlapping positions in the stems (Fig. 36.) at least until *Lixus* sp. formed pupation chambers which were wider than the pith and closed off at their ends.

VAN DER MEER (1972) put forward a theory that faunal overlap may not equal competition and high overlap may exist because competition is absent. This could be the case with borer species of *S. pterophorus.* SCHOEVER (1970) and RATHCKE (1976) noted the difficulty in measuring niche overlap. The overlap or competition could not be easily determined in this case but is probably represented by burrow positions in the stems. Volume of the stem was more than enough for various combinations of the three borer species because stems of infested plants were never totally consumed and the presence of the borers did not seem to affect the plants to the point of dying nor was there evidence of death of a borer due to the presence of another. It appears *S. pterophorus*'s defences reduced or influenced the number of herbivores such that no competition among borers was experienced.

There appeared to be some regulation of the number of borers of the same species per plant - no more than three were found in the same stem. Toxins, the difficulty encountered during entering the stem, or weather, could have eliminated a lot of weak larvae; or some were eaten by other insects to the correct carrying capacity of the host. Alternatively, the adult females did not lay more than about three eggs at a time, contrary to the observation by KRANZ *ET AL* (1978) of some *Lixus* species which lay many eggs in one place because instead of hosting other borer species, there would be instances of more than three larvae of the same species. The controlled number of larvae / plant, no matter by what means, ensured a reduction of both intraspecific and interspecific competition at the important feeding larval stage, as well as the survival of borers and their host.

What prevented the species of Cerambycidae to develop further is a matter of conjecture. No dead larvae of Cerambycidae were found in any stage of development of *S. pterophorous* plants. Hence there was no evidence of larvae being parasitised or killed by other insects or plant toxins. It could be that its larvae left the plant to pupate elsewhere such as in the soil or dead plant material. Other factors of the environment must have been right for its development since there must have been adults all the time which were depositing the eggs into *S. pterophorus*. The species of Cerambycidae may have been trying to colonise *S. pterophorus* for the first time or it could be that *S. pterophorus* was closely related to its original or real host.

Although the effects of borer herbivory were not determined the host plants never appeared to be under any stress from these borers. The borers did not show any ability to control the population of *S. pterophorus.* Instead, there was an equilibrium which was on one hand enhanced by seasonal effects upon the borers, and on the other hand, by the rate of growth of the particular host. It seemed as if the growth rate of the host determined the growth rate of the borer. Young borers were found in young hosts, and, while the hosts continued to grow throughout the four seasons, adults of the borer species emerged mainly during the warmer months. This meant that there was a break in the borer population - the proceeding generation had to come into being after or during the warmer seasons. The break in generation is clearly illustrated by Figs. 29, 37 and 38.

Appendix III gives a further explanation of why *Lixus* sp. could have opted for positions as indicated by Figs. 30, 31, 32, 33 & 36 and why *Mordella* may have required the upper parts of the stem as indicated by Fig. 34 and 36. Appendix III shows that the pith started appearing well above ground level and became widest somewhere around the middle of the stem while the stem was growing narrower from the bottom to the top. The wider diameter of the *Lixus* sp. larva required therefore the middle position of the stem and Appendix III shows that *Lixus* sp. burrows occupied the widest part of the pith. It can also be seen that the thickness of the vascular system of the stem, i.e. width between the pith and the bark of the stem became thinner towards the shoot. This position was suitable for the smaller *Mordella* sp. Furthermore, synchronisation, overcoming the hardened woody stem, and being able to detoxify or resist the alkaloids of *S. pterophorus* altogether, meant that the three borer species had to be specialised upon *S. pterophorus.* As a sign of this specificity solitary hosts were found to be infested by the borers, especially *Lixus* sp. It is perhaps this specialisation that paradoxically reduced the host range of the borer species such that they could not recognise *S. inaequidens* and other plant species as food. The three borer species could, and had to, identify *S. pterophorus* as their host using features that are unique to *S. pterophorus*, such as its kind of alkaloids and the nature of the leaf and stem surface which were, as pointed out in Chapter 1, quite different from those of *S. inaequidens.*

The reason that was advanced in Chapter 4 for the absence of borers in *S. inaequidens* was the fact that *S. inaequidens* had a pith too narrow for *Lixus* sp. and Cerambycidae to fit into while it had a very thin vascular system of the stem to be able to accommodate the pupation chambers of both *Lixus* sp. and *Mordella* sp. But since *S. inaequidens* is not poisonous and has a non-woody stem, why are there are no smaller borer species in a desirable host. There are two basic reasons why *S. inaequidens* had no borers. The first was that it had a very short life span. If the quality of pith was the same as that of *S. pterophorus*, then there could not be enough time for the borer to develop fully. Therefore, the short lifespan of *S. inaequidens* was its main defence against the borer species which are usually long lived beetles. The second reason why *S. inaequidens* could have been rejected by the borer species was its lack of apparent defences. Defences against herbivory which were identified on *S. pterophorus*, were overcome by the borer species but acted as barriers against those insect herbivores which failed to overcome those defences. The borer species may have consistently co-evolved with *S. pterophorus* (or other similar host species) and ended up with limited competition for *S. pterophorus* as a food resource and as a shelter. This suggestion was put forward by various researchers working on other insect - plant associations. (SOUTHWOOD *ET AL* , 1979; HODKINSON & HUGHES, 1982; STRONG *ET AL,* 1984)

It is not clear into what stage of development of *Lixus* sp. the parasitoids laid their eggs. The adult parasitoids were however seen frequenting on flowering plants of *S. pterophorus.* The adult parasitoids had either just emerged or were looking for *Lixus* sp. to deposit their eggs. Flowering plants of *S. pterophorus* were host to mature larvae, pupae or adults. But larvae of *Lixus* sp. were found parastised - meaning that parastoids did not infest pupae. There is also a strong possibility that parasitoids laid their eggs into mature larvae of *Lixus* sp. which would not only have created a pupation chamber very close to the bark of the stem, but could reveal their presence by the loud tapping they made when disturbed, as described earlier.

That *Mordella* sp. larvae could attach themselves on any solid surface, gave this borer species the ability to move inside wider burrows of *Lixus* sp. and of the species of Cerambycidae or inside mature host plants whose pith had disintegranted. The larvae could perhaps be able to move from one host to another in case this was necessary.

The exact effect on the host plant of the shoot destruction, or of the presence of a gall due to infestation by *Lixus* sp. needs to be investigated further.

7 DISCUSSION

7.1 INTRODUCTION

The aim of this research was to compare the insect herbivores of two ecologically and taxonomically related plant species, *S. pterophorus* and *S. inaequidens*.

The two plant species shared generalist insect herbivores. In Chapter 4 it was shown that *S. pterophorus* had more herbivorous insect species but a smaller number of individual herbivores. It had also more serious insect herbivores, in the form of borers possibly as a result of having a thicker stem and a longer lifespan. More sap suckers were found upon the softer plant species, *S. inaequidens*. The dry mass of *S. pterophorus* increased significantly during the sampling period due to the secondary growth while that of S. *inaequidens* was not seasonal. (Chapter 5). The overall number of insect herbivores was not seasonal and was not therefore correlated with the dry mass of the two host species. The more important insect herbivores which were seasonal were also not correlated with the dry mass of their hosts. Seasons affected these insect herbivores directly rather than via their two host species.

Chapter 6 gave observations on three borer species of *S. pterophorus* which never appeared upon *S. inaequidens.* There was no evidence of competition between the borer species nor did the borers seem to affect their hosts to the point of controlling their populations. The borer development was synchronised with that of its individual host.

7.2 POSSIBLE USE OF THE RESULTS

The results as summarised above can be used to highlight some of the differences or similarities between S. *pterophorus* and S. *inaequidens.* An attempt to analyse the results in light of various ecological, taxonomical and evolutional theories is also made toward the end of this section. None of the insect herbivores that were found can be utilised to control the two plant species because many of them were polyphagous - for biological control using insect herbivores it might be necessary to locate and visit the original or other regions where the two plant species are found.

7.2.1 DIFFERENCES

The recruitment of borers and a bigger number of herbivorous insect species by S. *pterophorus* emphasised some of the physical or structural characteristics of S. *pterophorus* which were mentioned in Chapter 1 and Chapter 3, but which were not possessed by S. *inaequidens.*

It was indicated in Chapter 3 that S. *pterophorus* was a more robust plant species than S. *inaequidens.*

The borer species exploited the robust nature of the plant in that their larvae could fit inside the stems of *S. pterophorus*. The width of the larvae of *Lixus* sp. (Chapter 6) would be larger than the width of the stem of *S. inaequidens* (Chapter 3): The stem of *S. pterophorus* was of such a volume that it could accommodate three borer species with no apparent competition between them. The borer species also contributed towards the higher number of herbivorous insect species found upon *S. pterophorus* (Chapter 6) since they were not shared. It was also stated in Chapter 3 that *S. pterophorus* had a longer life cycle, that it competitively persisted into early climax ecosystems as well. The borer species required a longer period of development than that of *S. inaequidens.* Of the two plant species *S. pterophorus* would be preferred by the borer species in order to complete their life cycles successfully.

Chapter 4 showed a higher number of insect herbivores upon *S. inaequidens* than on *S. pterophorus.* This might imply that herbivores were attracted to the former plant species because it was not only softer but, as indicated in Chapter 1, (page 2) was less or not at all chemically protected despite the fact that *S. inaequidens* was less apparent, both due to its smaller size and to its shorter lifespan. *S. inaequidens* was not woody (Chapter 3) and so recruited more stem sap suckers (Chapter 4), while the presence of trichomes upon the leaves of *S. pterophorus* was possibly responsible for the fewer insect herbivores upon the foliage of *S. pterophorus.*

Various researchers who have done, probably, more comprehensive surveys involving weeds reported in GOEDEN AND RICKER (1967) contended that if polyphagous insects are recruited their host is most probably not indigenous in that area. Similar views were given by STRONG *ET AL* (1984) GOEDEN AND RICKER (1976, 1986) who added that introduced plants tend to host polyphagous and often ectophagous insects or host less endophagous species and lack monophages while colonisation by endophages takes longer. These views were also supported by OLCKERS (1988) here in South Africa. *S. inaequidens* hosted polyphagous and ectophagous insects mainly suggesting that it was probably a later recruit to the Butterworth environment compared to *S. pterophorus* which recruited not only a bigger number of species of insect herbivores but also more specialised endophagous species along with their parasitoids.

7.2.2 SIMILARITIES

Both plant species were opportunists that occupied disturbed areas. (Chapter 3). Their populations were determined more by availability of bare soil than by season (Chapter 3 and Chapter 5). Therefore most of the insect herbivores found upon the two plant species could be expected to be generalists. Lack of the more specific insect herbivores was a further indication of the unpredictability of finding the two plant species both in space and time. In space because of the fact that the location of disturbed areas had no regular pattern and in time because the two plant species were not seasonal. The sharing of generalists was most likely related to the ecological similarity as well as the taxonomic relatedness of the two plant species. The two plant species recruited one serious similar species of herbivores exclusively to themselves that would also indicate some taxonomic relatedness.

Monolepta sp. appeared on only these two plant species in the study area. *Monolepta* sp. might have been identifying the two plant species by a characteristic common to the two plant species, but probably not found on other plant species in the area. However, food identification and preferences of *Monolepta* sp. need to be studied further so that the characteristics which *Monolepta* sp. identifies and their relative importance in the classification of plants can be known. Besides, the two plant species did not recruit other herbivores exclusively to themselves; other than *Monolepta* sp. So their taxonomic relatedness to a finer detail cannot be judged upon sharing only one insect species. The theory of HODKINSON AND HUGHES (1982) (page 4) could not be tested.

Both *Senecio* species generally supported a narrow diversity of insect herbivores compared to those of other plants taken from other families. This may imply that the genus *Senecio* is in relation to other plant taxa, effectively, although not equally morphologically and chemically well protected. This may have contributed to the apparently extensive occupation of pioneer ecosystems around Butterworth, by *S. inaequidens* and *S. pterophorus*.

Insect herbivores of the two *Senecio* species had a wide host range and few were monophagous or endophagous. These are characteristics of introduced plants (GOEDEN AND RICKER [1976] SOUTHWOOD ET AL [1984], and OLCKERS [1988]). The two plant species may therefore be exotic at Butterworth. However, additional data from other parts of South Africa and other parts of the World is needed to justify this statement, and the number of species of insect herbivores associated with other plant species around Butterworth needs to be investigated in order to eliminate the possibility that the low numbers of herbivorous insect species associated with *S. inaequidens* and *S. pterophorus* could be due to environmental factors. For example, it is likely that purely pioneer plant species may recruit polyphagous and ectophagous insect herbivores mainly because such plants are temporary and the pioneer environment is often devoid of shelter from weather extremes as well as relatively permanent alternative hosts.

7.3 CONCLUSION

The unpredictability of the two plant species in terms of where and when they appear could give protection against herbivory although they could still be open to exploitation by generalist herbivores. There is no prospect of controlling these two plant species at Butterworth by means of their insect herbivores that were found in Butterworth.

The number of species of insect herbivores can reflect the number of micro habitats or the lifespan of the host.

The nature of insect herbivores can be used to emphasise characteristics of their hosts or alternatively the kind of insect herbivores that can feed upon a given plant species can be predicted by analysing the anatomy and the ecology of that plant. By comparing insect herbivores recruited, the taxonomic differences, but not the similarities, can easily be identified. Taxonomic similarities can be highlighted by a more detailed study, especially involving the host range of the shared insect herbivores. The study would have improved to the extent of analysing some theories of ecology and evolution if:

i) Samples were taken more frequently.

ii) Bigger numbers of plants were sampled.

iii) The study had lasted longer.

iv) Other sites further away from Butterworth were sampled (i.e. other South African sites such as those in Natal and also on other Continents) - this would perhaps help in identifying the origins of the two plant species.

7.4 SUGGESTED FURTHER RESEARCH

i) Insect herbivores of *S. pterophorus* and *S. inaequidens* (in any other region) compared to those around Butterworth.

ii) The biology of *Lixus* sp.

8.0 APPENDICES.

8.1 APPENDIX I

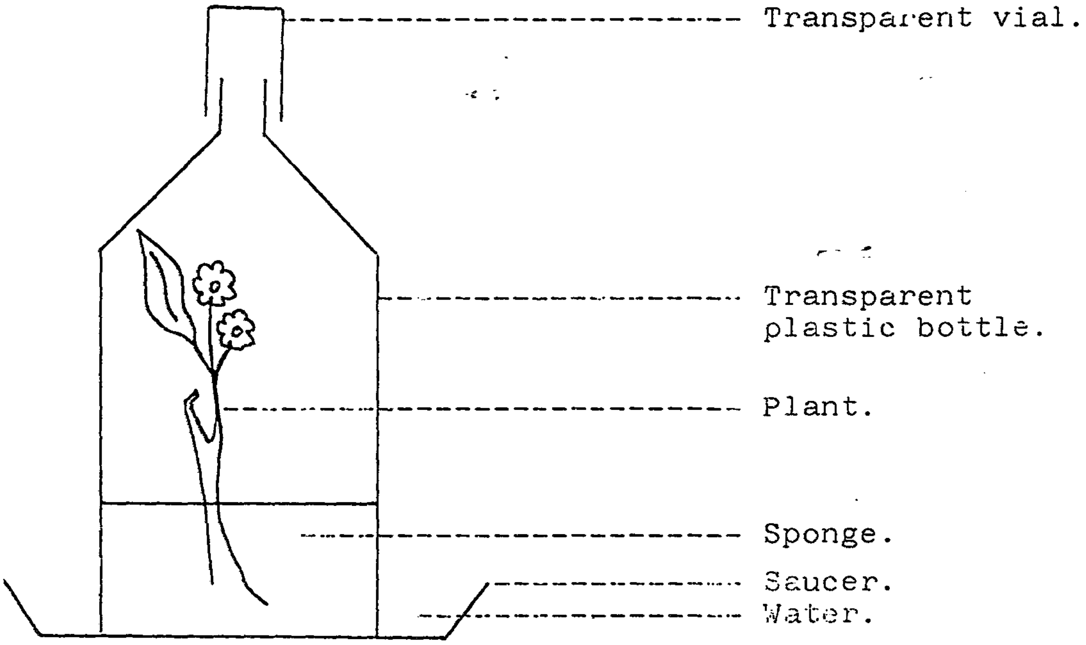


Fig 1. **Method used to preserve plant material for rearing insects. (Refer section 2.3.1)**

8.2 APPENDIX II

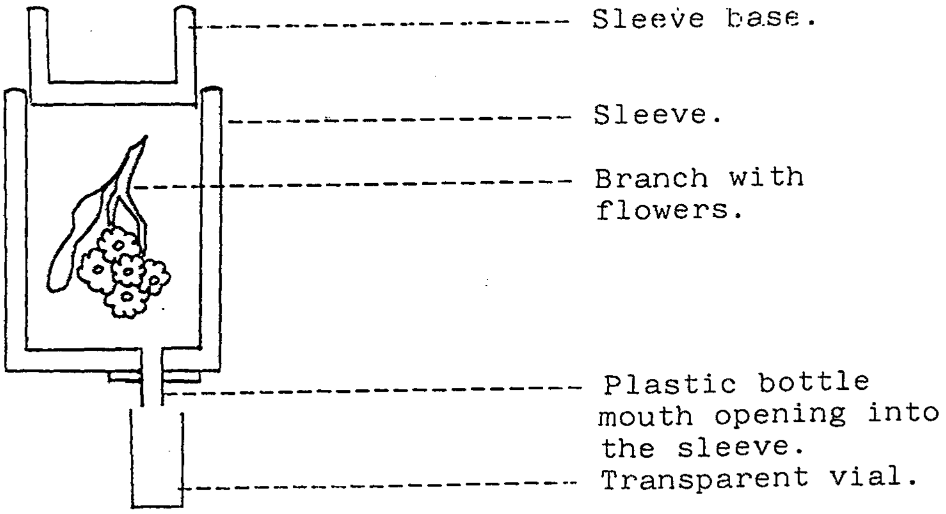


Fig. 2. **Emergence bottle for flower insects. (Refer section 2.3.2)**

8.3 APPENDIX III Relative width of stems and pith at different height intervals of flowering plants of *S. pterophorous.* (four borer plants were sampled) units are in millimetres.

Plant (a)

Height from the ground	Stem width	Pith width	No. of branches at that height
32,0	20,0	3,0	-
73,0	16,0	4,0	-
159,0	15,5	5,0	-
267,0	15,0	5,5	-
374,0	14,5	5,5	10) Position of burrows
505,5	12,5	5,5	22) of *Lixus sp.*
756,5	10,0	5,5	23
1021,5	6,0	5,0	6
1363,5	3,3	3,0	3
1368,0	0,0	0,0	0
Plant (b)			
0,0	33,0	0,0	-
13,0	27,0	1,0	-
84,0	22,0	6,0	-
167,0	17,0	6,0	6) Position of burrows
237,0	17,0	6,0	6) of *Lixus sp.*
368,0	11,0	5,5	10
485,0	10,0	5,0	9
620,0	8,0	5,0	10
788,0	7,0	4,5	2
960,0	4,0	2,0	10
1109,0	1,0	0,5	7
1112,0	0,0	0,0	-
Plant (c)			
0,0	28,0	0,0	-
88,0	16,0	4,5	8
192,0	15,5	4,0	4) Position of burrows
293,0	15,5	4,5	7) of *Lixus sp.*
419,0	10,5	2,5	7
522,0	7,5	2,0	3
651,0	5,0	2,0	12
796,0	3,0	1,5	17
911,0	1,0	0,5	5
915,0	0,0	0,0	-
Plant (d)			
0,0	10,0	0,0	-
65,0	8,5	4,0	-
200,0	10,0	4,0	-
345,0	10,0	2,0	-
655,0	1,0	0,5	-
675,0	0,0	0,0	-

9.0 REFERENCES

Adamson, R.S. & T.M. Salter. 1950 *Flora of the Cape Peninsula* Juta, Cape Town.

Annecke, D.P. & V.C. Moran. 1982 *Insects and mites of cultivated plants in South Africa.* Butterworths, Durban.

Daly, R.H., Doyen, J.T. & P.R. Ehrlich. 1978 *Introduction to insect biology and diversity.* McGraw - Hill, Kogugusha Ltd., Tokyo.

De Wet, C. 1991 Correspondence. National Botantical Institute, P/B 101, Pretoria 0001.

Eliovson, S. 1973 *South African wild flowers for the garden.* Dai Nippon Printing Company Ltd., Hong Kong.

Everett, T.H. 1980 *The New York Botanical Gardens : Illustrated Encyclopaedia of Horticulture. Vol. 9.* p. 3132, Garland, New York.

Fourie, D. 1991 Correspondence. National Botanical Institute, P/B X101, Pretoria 0001.

Fowler, S.V. 1985 Differences in insect species richness and faunal competition of birch seedlings, saplings and trees. *Ecological Entomology 10.* p. 159 - 169.

Goeden, R.D. & Ricker, D.W. 1967 The phytophagous insect fauna of the Russian thistle (*Salfola Kali* var. *tenuifola*) in southern California. *Annals of the entomological society of America Vol. 61 No. 1* : p. 67 - 72.

Goeden, R.D. & Ricker, D.W. 1976 The phtophagous insect fauna of the Ragweed. (*Ambrosia psilostachya*) in southern California. *Environmental Entomology Vol. 5 No. 6* : p. 1169 - 1177.

Goeden, R.D. & Ricker, D.W. 1986 Phytophagus insect faunas of two introduced *cirsuim* thistles, *C. ochrocentrum* and *C. vulgare* in Southern California. *Annals of the entomological society of America* : p. 953 - 962.

Goodwin, T.W. & Mercer, E.T. 1983 *Introduction to Plant Biochemistry. 2nd Edition* Pergamon Press, Oxford.

Guillarmod, A.J. 1971 *Flora of Lesotho (Basotholand)* Verslag van J. Cramer, Lehre, 3301.

Gulick, B.A., Irwin, K.M.L., Quallis Jr. W.C., Gribble, D.H., & Quinton, R.R. 1980. Effect of pyrrolizine alkaloid - induced hepatic disease on plasma amino acid patterns in the horse. *American Journal of Veterinary Research 41/11* : p. 1894 - 1898.

Harris, P. 1973 The selection of effective agents for the biological control of weeds. *Canadian entomologist 105* : p. 1495 - 1503

Hilliard, O.M. 1977 *Compositae in Natal* University of Natal Press, Pietermaritzburg.

Hodkinson, I.D. & Hughes, M.K. 1982 *Outline Studies in Ecolocy* : *Insect herbivory.* Chapman and Hall, London. New York.

Huelbusch, K.H. & Kuhbier, H. 1979 Sociology of *Senecio inaequidens.* New Records (Translated). *ABH Naturwiss ver Bremen 39 (1/6)* : p. 47 - 54.

Jackson, W.P.U. 1977 *Wild Flowers of Table Mountain* Howard Timmins, Cape Town.

Kalule - Sabiiti, 1991 Correspondence. Assistant Director, Agricultural Research, Department of Agriculture and Forestry, Umtata. - Transkei Region.

King, L.J. 1966 *Weeds of the World* : *Biology and Control.* Interscience Publishers Inc., New York.

Lawton, J.H. & Schroeder, T.W. 1977 The effect of plant type, size of geographical range and taxonomic isolation of the number of insect species associated with British plants. *Nature 265* : p. 137 - 140.

Mabberley, D.J. 1987 *The plant book : A portable dictionary of the higher plants.* Cambridge University Press, Cambridge.

Moran, V.C. 1980 Interactions between phytophagous insects and their *Opuntia* hosts. *Ecological entomology 5* : p. 153 - 164.

Olckers, T. 1988 Biological studies of insect herbivores associated with some species of *solanum. Thesis submitted to Rhodes University for the degree of Doctor of Philosophy.*

Rathcke, B.J. 1976 Competition and co-existence within a guild of herbivorous insects. *Ecology 57* : p. 76 - 90.

Small, J. 1966 *The origin and development of Compositae.* Wheldon and Wesley Ltd., Hitching Herts., England.

Southwood, T.R.E. 1961 The number of species of insects associated with various trees. *Journal of animal ecology 30* : p. 1 - 8.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. 1979 The relationships of plant and insect diversities in succession. *Journal of Linnius Society 12* : p. 327 - 348.

Southwood, T.R.E., Moran, V.C. & Kennedy, C.E.J. 1982 The richness, abundance and biomass of the arthropod communities on trees. *Journal of animal ecology 51* : p. 635 - 649.

Stinson, C.S. & Brown, V.K. 1982 Seasonal changes in the architectural plant communities and its relevance to insect herbivores. *Oecologia (BGI) 56* : p. 61 - 69.

Strong, D.R., Lawton, J.H. & Southwood, T.R.E. 1984 *Insects on plants : Community patterns and mechanisms.* Blackwell Scientific Publications, London.

Swanevelder, C.J., Els, W.C., Hanekom, F., Kotze, J.C., Myburg, D.W., Van Fradenburg, L.P. & Van Huysteen, M.K.R. 1975 *Senior Geography Std._10* Nasou, Cape Town.

Vahrmeijer, J. 1981 *Poisonous plants of Southern Africa that cause stock losses.* Tafelberg Uitgewers Beperk, Cape Town.

Van der Meer, J.H. 1972 Niche Theory. *Annual review of Entomoloy 3* : p. 107 - 132.

Varley, G.C., Gradwell, G.R. & Hassell, M.P. 1973 *Insect population ecology - An analytical approach.* Blackwell Scientific Publications, Osyney Mead, Oxford.

Webster's Dictionary, 1981 Vol. III

Wells, M.J., Balsinhas, A.A., Joffe, H. Engelbrecht, V.M., Harching, G., & Stimon, C.H. 1986 A catalogue of problem plants in Southern Africa. *Memoirs of the botanical survey of South Africa No. 53.* Botanical Research Institute, Dept. of Agriculture and Water Supply, South Africa.